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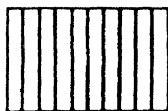
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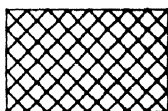
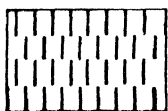
STEMS AND PETIOLES

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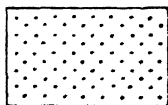
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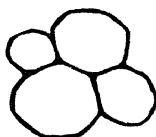
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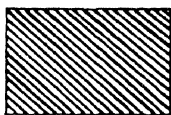
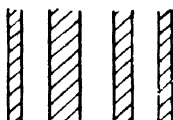
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WOOD

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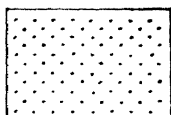
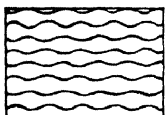


RAYS



— **PARENCHYMA**

SEPTATE FIBRES



— **PHLOEM**

TRACHEIDS



SCLERENCHYMA

The above types of shading have been used for the tissues in the drawings which have been specially prepared for this book. They do not apply to drawings where an author's name is given. Septate fibres not shaded except where forming patches in the ground-tissue of the wood. Transverse sections of Wood $\times 50$, Rays $\times 90$.

ANATOMY OF THE
DICOTYLEDONS

ANATOMY OF THE DICOTYLEDONS

*LEAVES, STEM, AND WOOD
IN RELATION TO TAXONOMY
WITH NOTES ON ECONOMIC USES*

BY

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FOREWORD

It is more than forty years since L. A. Boodle, then in charge of the Jodrell Laboratory, and F. E. Fritsch, then also working at Kew, collaborated in the translation of Solereder's work on the systematic anatomy of the Dicotyledons. Boodle brought to this task a profound knowledge of the subject, acquired in the course of his official duties, which gave to the translation an even greater value than that of the German original. During the past forty years the range of material available for study has been greatly augmented, and a large mass of data has been accumulated at Kew, which has enabled generalizations to be based on a surer foundation and provided the means of filling many of the gaps in Solereder's work. In this task Dr. Metcalfe, who succeeded Boodle in the charge of the Jodrell Laboratory, has ably carried forward the work which Boodle began, to such good purpose that the present publication must be regarded as a new work incorporating and correcting the old, and in a far more real sense as a comprehensive survey of the anatomical features of dicotyledonous plants considered as taxonomic characteristics.

In no aspect of plant anatomy has more extensive progress been made during the past half-century than in the study of the secondary wood, in no small degree because of the growing appreciation of the importance of anatomical characters for the identification of commercial timbers. It is therefore a pleasure to record the debt to Dr. L. Chalk who has collaborated in the production of this work and to whom the original descriptions of the secondary woods are entirely due.

The whole constitutes a monument to the assiduous labours of the authors and will long remain the standard reference work on the subject and indispensable to every Botanical Library of any importance.

The living collections at Kew, now numbering some 45,000 species, have provided an invaluable source of material, but in addition specimens have been sought from all parts of the world, and there are but few larger groups of all the vast assemblage of dicotyledonous plants that have not been examined in respect to one or more representatives. The large collection of wood specimens and microscope slides at the Imperial Forestry Institute, Oxford, formed the basis of the work on wood anatomy, and this was supplemented by data specially collected by Dr. M. M. Chattaway for all the genera in the Yale Collection not available in Oxford. Thus the picture of the range of structure evolved by the various taxonomic groups is presented with a completeness that was never before possible and with a simplification of treatment that a mastery of detail can alone achieve.

E. J. SALISBURY

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KEW

PREFACE

THIS reference book aims at providing a summary of our present knowledge of the anatomy of the vegetative organs of the Dicotyledons. It has been written mainly so as to emphasize the taxonomic and phylogenetic value of histology, thus perpetuating and extending Solereder's chief aim when he wrote his *Systematic Anatomy of the Dicotyledons*, of which the English translation was published in 1908. At the same time the authors hope that botanists who are interested in other aspects of the anatomy of the Dicotyledons will find the book useful as a work of reference. Some attention has accordingly been devoted to ecological and developmental anatomy, and references have been included in the bibliography which should enable workers to find more detailed information concerning these subjects. In addition an attempt has been made to appeal to a wider range of readers by including, under many of the families, a section headed 'Economic Uses'. In particular it is hoped that this will be of interest to pharmacognosists, foresters, wood technologists, public analysts, and all who have to deal with plant products of economic importance and their microscopical structure. Since the book is concerned solely with the anatomy of the vegetative organs, the microscopy of economic products derived from flowers or fruits has been omitted.

Although British taxonomists frequently recognize the value of attempting to investigate taxonomic problems along anatomical lines, this method is seldom practised in the herbarium. This is partly because herbarium botanists are so few that they are very hard pressed to complete their everyday work of identification and description of new species. Furthermore it is very seldom that an herbarium botanist receives more than a very elementary training in plant structure, so that he lacks the confidence and knowledge which are necessary to assess the value of anatomical characters. In Britain, the relationship between plant structure and physiological function or environment has commanded more attention than that which exists between structure and taxonomic affinity. Herbarium botanists on the European continent have devoted more attention to systematic anatomy, while it is well known that the Englerian system of classification is partly based on anatomical characters observed by continental taxonomists. In recent years there has been a world-wide interest in the systematic anatomy of the secondary xylem, but this subject has been investigated largely by specialists whose basic training has been in forestry or wood technology rather than in taxonomy. This has had two consequences: (i) that herbarium botanists find the need of some authoritative guidance in interpreting the anatomical evidence; (ii) that anatomists tend to be segregated into those with a knowledge of wood structure and those who are familiar with the structure of other parts of the plant body. In order to meet these two defects a book is required in which the combined knowledge of the general systematic anatomist together with that of the specialist in wood structure is summarized and presented in a form which can be generally understood by anatomists, and its taxonomic significance made clear to the herbarium botanist.

We undertook to write this book in the hope that a modern counterpart to

Solereder's well-known treatise on the same subject would lead towards a more natural classification of the Dicotyledons and make some contribution to our knowledge of phylogeny. Although we had felt for many years that a reference book of the kind we have written was badly needed, and had indeed been recording facts and making reference collections of microscope slides with some such purpose in mind, it was not until after a meeting of the Systematics Association in 1938 that the late Sir Arthur Hill, then Director of Kew, raised the question of publication with the Delegates of the Clarendon Press. The task of writing the book was started in 1939.

In writing the descriptions of the 'Leaf' and 'Stem' which constitute a large part of the present book, Solereder's previous treatise has provided the starting point, and, indeed, were it not for the assistance derived from this source, our task would not have been completed for many years. The facts obtained from Solereder's book have been combined with those obtained from work published in journals and books since 1908 and further expanded by a large number of original observations. The information thus accumulated is presented in as concise a form as possible. Solereder's somewhat ponderous style has undoubtedly deterred many botanists from using his treatise or fully appreciating the value of its contents. The more condensed mode of presentation now adopted has necessitated the omission of some of the exceedingly detailed information included in Solereder's book and in the subsequent literature. It seemed to the authors, however, that it is preferable for specialists studying certain families or groups to consult the original sources for such details. For this reason a very full bibliography to literature that has appeared since 1908 has been included, whilst references to the older literature that may be found in Solereder's book have been omitted.

Solereder fully realized and stressed the taxonomic importance of wood structure. A justifiable criticism of his book, however, is that most of his remarks on this subject refer to the wood of small twigs such as occur in herbarium specimens rather than to samples which may be described as 'timber'. The microscopical features of the wood from young twigs frequently differ considerably from those visible in wood specimens of the type which are the special concern of the forester or wood technologist. In the present work we have, as far as possible, drawn a clear distinction between the xylem of young twigs, which is described under 'Stem', and the wood of the forester's sample, which is described under 'Wood'.

The illustrations include some of those which appeared in Solereder's book, but as his treatise has been frequently criticized because they were so few, very many new ones have been added. The new drawings are intended to show diagrammatically the structure of young stems and petioles in transverse sections, of the wood in transverse sections ($\times 50$), and of the medullary rays of the wood in tangential sections ($\times 95$). The species illustrated have been selected in order to indicate the range of structure in each family, so far as the material available to us has made this possible. This has frequently meant that little-known species have been illustrated in preference to those which are more generally familiar or of greater economic importance. The authors believe that this course will be found more valuable, from the scientific point of view, in a book which is basically taxonomic. Almost all of the new illustrations are original, and have been drawn from slides in our

respective reference collections. The authors are particularly indebted to Dr. C. L. Hare for his painstaking assistance in preparing and arranging a large part of these drawings, many of which are solely his own work. Thanks are also due to Mr. J. S. Shaw who prepared for the press many of the drawings of the wood made by Dr. Chalk. More recently considerable assistance in the arrangement of the drawings has been received from Miss E. M. Slatter and Mr. F. R. Richardson.

We are greatly indebted to our numerous friends and colleagues for their encouragement, helpful suggestions, and criticisms throughout our long task. When the work began, many of the preliminary descriptions of the wood structure were ably drawn up by Dr. M. M. Chattaway. Later Dr. C. L. Hare worked systematically through a large proportion of the reference collection of slides at Kew, recording his observations in the form of notes and tables which have been of the greatest value when writing the text. We are especially grateful to these two workers for their collaboration. As neither of the authors is an expert in systematic botany it has been necessary to make frequent calls on our taxonomic colleagues for their assistance. In the early stages of our work we were helped particularly by Dr. T. A. Sprague and Dr. W. B. Turrill, and later on by Dr. J. Hutchinson, F.R.S. Taxonomic advice concerning certain groups has also been given by Mr. H. K. Airy-Shaw, Mr. N. Y. Sandwith, and other members of the staff of the Kew herbarium. The work at the Jodrell Laboratory could not have been completed so soon without the energy, patience, and skill which Mr. F. R. Richardson devoted to preparing many thousands of microscope slides of material cultivated in the gardens or housed in the reference collections in the Kew museums and herbarium. We are also indebted to the gardens staff at Kew for the large quantities of living material which they were able to supply, to Major A. A. Dorrien Smith, D.S.O., for living specimens from his gardens at Tresco in the Isles of Scilly, and to Mr. E. Nelves for his assistance in preparing the index.

The work on wood anatomy has been made possible by the large collection of microscope slides at the Imperial Forestry Institute, Oxford, and, though it is impossible to list all those who have helped to build up this collection, mention must be made of the Forest Products Research Laboratory, Princes Risborough (Mr. B. J. Rendle), the Yale School of Forestry (Prof. S. J. Record), the Forest Research Institute, Kepong, Malaya (Dr. H. E. Desch), and the Forest Department, Gold Coast Colony (Mr. C. Vigne) for their exceptionally valuable contributions of material, and of Mr. A. A. Shaw, Mr. C. W. Bond and Mr. P. Franklin for their assistance in preparing the slides.

January 1950.

C.R.M.
L.C.

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INTRODUCTION

ANATOMY AND TAXONOMY

THE historical development of botany has been such that physiological and anatomical investigations of plants have been unnecessarily separated from studies of systematic arrangement, and workers in these artificially divided fields have developed their own special techniques and outlooks. From time to time anatomists, though in general more interested in structure in relation to function than to classification, have made excursions into the realms of taxonomy, and have added some solid contributions to the knowledge of systematy. In general, however, the work of anatomists has tended to be overlooked or mistrusted by their taxonomic colleagues. The chief reason for this is that anatomists have not always realized the limitations of their mode of investigation and have sometimes drawn conclusions that, to a taxonomist, are obviously highly improbable. Conversely many highly skilled taxonomists have sometimes been unable to assess the value of anatomical investigations. There have been signs in recent years, however, that as taxonomists have learned the value of co-operation with cytologists and geneticists, so they are coming to appreciate the contribution which anatomists can make to their investigations. At the same time anatomists are ready to admit that anatomical characters cannot by themselves form the basis of classification, but are to be regarded rather as an extension of, and supplement to, those external morphological characters on which classifications have been built.

Practical Reasons for Using Anatomical Characters

The taxonomic value of cytological and genetical studies lies chiefly in the interpretation of species and groups of lower rank. Anatomical structure, on the other hand, is most likely to provide evidence concerning the inter-relationships of larger groups such as families, or in helping to establish the real affinities of genera of uncertain taxonomic status. Anatomy is of restricted value for distinguishing species or groups of less than specific rank, because the differences between them are usually quantitative rather than qualitative, and often demand statistical treatment based on a greater amount of material than is frequently available.

Anatomy sometimes proves very helpful for individual identifications. For example, microscopical methods are of great value in establishing the identity of herbarium specimens which are not accompanied by flowers or fruits. That this can frequently be done has repeatedly been proved at Kew, when, by microscopical examination, it has been possible to assign sterile specimens to a family or genus, thus greatly simplifying the task of the herbarium botanist. Microscopical methods are also often necessary to establish the botanical identity of commercial samples of medicinal plants, timbers, fibres, &c., and may play an important part in checking adulteration, substitution, and fraud, and have on occasion been instrumental in helping to establish the guilt or innocence of suspected criminals. These practical applications alone provide sufficient cause to justify the use of anatomical methods in taxonomic

investigations. Finally it may be pointed out that a complete anatomical survey is necessary as a preliminary to the interpretation of palaeobotanical remains.

Characters of Taxonomic Importance

It will be readily appreciated that the taxonomic value of anatomical characters is inversely proportional to their plasticity, those which are particularly liable to become modified in response to environmental change being most unsatisfactory. On the other hand no characters are strictly immutable. In practice, however, many characters are more fixed than others, and it is on those that are less plastic that the systematic anatomist must rely. It should also be realized that conclusions supported or suggested by *combinations* of characters are more likely to be correct than those which rest on one character alone.⁶ The feature or features to be employed will, however, depend on the nature of the material to be examined as well as on the taxonomic problem to be settled. For instance, an entirely different method of approach would be necessary if the problem were to determine to what family a leafy twig belonged, compared with the procedure a pharmacognosist would adopt when distinguishing between the leaves of two species of *Digitalis*. In solving the second problem differences in the exact type and structure of the trichomes would be of importance whilst one could also make use of measurable differences such as those of the vein-islet number. In attempting to deal with the first problem qualitative differences would be more important. Dimensions are generally more liable to vary with conditions of growth than are differences in kind, and should therefore be used with great caution when attempting to separate species on anatomical grounds.⁷ For example, a distinction between two species based on the density of the hairs on the leaves or on stomatal size and frequency is not likely to be satisfactory unless the differences are very marked, as these features vary with environment or even in different parts of an individual plant. Differences in the type of hair, on the other hand, usually provide much more reliable grounds for separation. Failure to appreciate the variability of dimensional characters has sometimes led to erroneous conclusions that have tended to bring the anatomical method into disrepute.

Plants which are not closely related to one another sometimes develop similar habit forms or structural features. For example, there are certain members of the Euphorbiaceae, Cactaceae, Geraniaceae, Compositae, and Apocynaceae in which a stem succulent habit has been evolved, presumably as a direct response to the dry ecological habitat of the plants in which they are exemplified. Corresponding anatomical similarities, such as enlargement of parenchymatous cells, have also arisen in the same plants. Although these anatomical resemblances possess diagnostic value because they occur in but few families, the greatest care must be taken to ensure that they are not by themselves taken as evidence of taxonomic affinity between the plants in which they are exhibited.

Many other examples of anatomical responses to ecological conditions could be cited. All of these are well known to those who are interested in ecological anatomy, but it is necessary to draw attention to a few of them, if only to emphasize that they must be carefully distinguished from characters possessing taxonomic value. Thus it may be noted that well-developed systems of

intercellular spaces are characteristic of aquatic plants. The structure of the mesophyll is also dependent on the nature of the habitat. For example, some of the plants in dry localities may possess small leaves of the ericoid type with inrolled margins, others such as some of the acacias have leaves in which the mesophyll is isobilateral, and in plants with cylindrical leaves the mesophyll is centric. Another variation sometimes occurs in species with adpressed leaves in which spongy tissue is developed towards the adaxial surface and palisade tissue towards the abaxial surface, thus reversing the arrangement which is characteristic of most leaves with a dorsiventral mesophyll. Ecological specializations that occur in stems include the specially large vessels in the xylem of climbing plants, and the ring-porosity of many woods from temperate regions.

Another difficulty, which the systematic anatomist must face, is that some very useful diagnostic characters, which have no apparent ecological significance, have arisen quite independently in unrelated families. The following examples will serve to illustrate this point.

Laticiferous elements are of restricted distribution and therefore of diagnostic value, but the possession of these structures does not necessarily imply affinity. They are to be found in such diverse families as Papaveraceae, Eucommiaceae, Compositae, and Euphorbiaceae. Intraxylary phloem is common to the closely related Apocynaceae and Asclepiadaceae and in this instance provides confirmatory evidence of affinity. It nevertheless occurs also in certain of the Lythraceae, Combretaceae, and Gentianaceae, as well as in many other families that are not closely related to one another. Here again it can be seen that intraxylary phloem is of taxonomic value because of its restricted occurrence, but it may or may not be indicative of affinity. A third example is afforded by the nature of the petiolar vascular system. If transverse sections be cut through corresponding regions (preferably immediately below the lamina) of the leaves of Dicotyledons, it will be found that the vascular systems can be arranged in a series of intergrading types; closely similar forms frequently occur, however, in quite unrelated families. Nevertheless, the different types of petiolar structure are of diagnostic value because of their restricted occurrence and relative stability.

It is important to realize that an anatomical feature which is of considerable diagnostic value in one family is not necessarily of equivalent value in another. This is not very remarkable when one recalls that the same principle applies when using exomorphic characters for taxonomic purposes. All families are not of equal status. Some consist of only one or a few genera, but many species, others of many genera, but few species. Besides this, families vary considerably in size, and the lines of demarcation between them are largely a matter of personal opinion, since no absolute criteria for their separation exist.

It is sometimes averred that the use of anatomical characters is undesirable because this practice will lead to taxonomic conclusions completely at variance with those that are now generally accepted. Experience shows, however, that this is by no means wholly true. Many anatomical characters indicate relationships in harmony with those suggested by exomorphic features including those of the flower. Where exomorphic and anatomical characters are alleged to point to different conclusions it will frequently be found that the discrepancy is due to an incorrect interpretation of the available facts. In cases of this kind

a joint reinvestigation by an anatomist and a systematist may quite well lead to readjustments more in line with those suggested by the anatomical characters. It is, however, most important to rely on anatomical characters of which the taxonomic value has become well established. These will now be enumerated.

1. HAIRS

The diversity of external hairs is familiar to all taxonomists. Firstly there are the glandular and non-glandular categories, each of which may be subdivided according to the number of component cells, degree of branching, and so forth. Whole families may frequently be recognized by the occurrence of one or more distinctive types of hair. In other instances hairs are of more value for the determination of species or genera. The length, size, and density of hairs are more liable to vary with environment than is the occurrence of different kinds, so that the former features are of more restricted taxonomic value. There are families, e.g. the Theaceae, in which hairs are infrequent and others, e.g. Cistaceae, in which they are abundant. Differences such as these are of value. Smaller variations in size and density should, however, be accepted as a basis for the separation of closely related genera and species only after exhaustive investigation of a wide range of material.

2. STOMATA

It is known that stomatal frequency not only varies from point to point in a single leaf but depends also on the level of insertion of the leaf on the stem, whilst it is also strongly influenced by the conditions prevailing in the habitat. It is scarcely surprising to find, therefore, that the number of stomata per unit area, and the extent to which they are raised above or sunk below the epidermis, is of very restricted importance compared with their appearance in surface view, especially the nature and orientation of the subsidiary cells in relation to the guard cells. The principal types of stoma are described in detail since they are of undoubted importance.

The term stoma is here taken to mean the pair of guard cells together with the aperture between them. When the cells immediately surrounding a stoma clearly differ from the remaining epidermal cells they are described as subsidiary cells.

The four main types of stoma which occur amongst the Dicotyledons are generally known respectively as 'ranunculaceous', 'cruciferous', 'caryophyllaceous', and 'rubiaceous'. These names are taken from the families in which they are well exemplified or in which they were first observed. It is now well known, however, that stomata of each of the above types occur in many other families besides those after which they were originally named. Another difficulty about the terms is that they have not always been used in exactly the same sense. They were originally applied to the mode of development rather than to the appearance of the stomata in a fully grown leaf, but since it is seldom possible, when identifying a small sample, to follow the development of stomata in detail, it has become usual to apply the terms to stomata as they appear when mature. For these reasons it seems very desirable to replace the present terms by new ones devoid of any taxonomic or ontogenetic implications. After consultation with Mr. H. K. Airy-Shaw the following new terms were devised and are put forward below for the first

time. If they prove to be generally acceptable, it is to be hoped that they will come into general use. Meanwhile the older and more familiar terms have been retained in this book to allow time for the new ones to become assimilated. Some additional descriptive terms for stomata will probably be found necessary in the future. For instance the so-called 'ranunculaceous' or anomocytic stoma includes a variety of types for which future investigation will probably provide a more satisfactory classification. Then again there are stomata surrounded by a circle of radiating cells which might appropriately be described as actinocytic.

Type A. Stoma surrounded by a limited number of cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis—the 'ranunculaceous' or anomocytic (irregular-celled) type.

Type B. Stoma surrounded by three cells of which one is distinctly smaller than the other two—the 'cruciferous' or anisocytic (unequal-celled) type.

Type C. Stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells—the 'rubiaceous' or paracytic (parallel-celled) type.

Type D. Stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells—the 'caryophyllaceous' or diacytic (cross-celled) type.

Reference must also be made to the so-called 'gramineous' stoma. This type does not really concern us, however, since it is believed to be confined to the Monocotyledons where it is especially characteristic of the Gramineae and Cyperaceae. The 'gramineous' stoma possesses guard cells of which the middle portions are much narrower than the ends so that the cells appear, in surface view, to be shaped like dumb-bells. The walls of the narrow portions of the guard cells are also strongly thickened, so that a transverse section passing through this region shows a narrow, slit-shaped lumen. There are frequently subsidiary cells as well lying parallel to the long axis of the pore.

Whilst the above classification of stomata is useful for diagnostic purposes, it should be realized that the various types tend to merge into one another. For example, it would be difficult to decide whether a stoma surrounded by three cells of equal or nearly equal size should be classed as ranunculaceous or cruciferous. It should also be remembered that stomata of more than one kind sometimes occur together on the same leaf surface, or stomata on the upper and lower surfaces respectively may not be alike.

3. EPIDERMAL CELLS AND HYPODERM

Epidermal cells differ considerably in size, shape, and outline in different plants, but external factors such as light intensity and atmospheric humidity often have a marked effect on these features. Their diagnostic value is further restricted by the fact that similar types of epidermal cell are often to be found in quite unrelated families. Nevertheless the shape of the epidermal cells provides useful confirmatory evidence, if the identity of a leaf is already suspected on other grounds. Characters such as a partly or wholly crystalliferous epidermis or the inclusion of cells with specific chemical contents, are of more importance because of their restricted occurrence. They must not,

however, be taken as indicators of affinity. Epidermal cells with vertical or horizontal partitions are likewise of specific or at most of generic value, since these features are of restricted and sporadic occurrence. A horizontally divided epidermis is not always easy to distinguish from a hypoderm, because the only difference between the two is that a true hypoderm is derived from the mesophyll in the course of development, whereas the divided epidermis, as its name implies, arises by partition of the epidermal cells themselves. When the cells of the outer and inner layers are opposite each other it is probably correct in most instances to assume that one is dealing with a divided epidermis, and, when this is not so, that the inner layer of cells is hypoderm. In a mature leaf the two features cannot be readily distinguished, but this is of no great practical importance, since, for taxonomic purposes, the occurrence of a hypoderm and a divided epidermis are of about equal value.

4. VEINS

In comparing the veins of two leaves, and in particular the structure of the vascular bundles and their relationship to the surrounding tissues, it is important to ensure that veins of the same order are being examined. Larger and smaller veins in an individual leaf often differ from each other to a considerable extent. Nevertheless certain characters of the veins are of confirmatory value in the identification of species and genera. For instance the vascular bundles of the veins may be wholly immersed in the mesophyll or raised above the general level of the upper or lower surface of the lamina. Alternatively they may be surrounded by a distinct parenchymatous sheath, or be partly or wholly enclosed by sclerenchyma. Veins in which the vascular bundles are accompanied on either side by parenchyma devoid of chlorophyll or by sclerenchymatous or collenchymatous tissue occupying the whole of the space between the bundle and the upper and lower epidermis are described as vertically transcurrent. The possession of this character is likewise of specific or generic value.

5. PETIOLE

The petiole is of considerable taxonomic importance, since its structure appears to be but little affected by environmental change. In comparing petioles by means of transverse sections, however, it is essential that sections of strictly comparable portions of the petioles in question are examined. The vascular system, in its passage through a petiole, frequently displays a complex and highly characteristic series of changes, so that sections taken at different levels in a single petiole may be very unlike one another. To obtain a complete picture of the vascular system of the petiole a series of sections must be cut, but since this operation requires more time than is frequently justified by the results, it has become customary to examine sections through the distal end immediately below the lamina, and to compare them with sections taken from the same position in other leaves. Supplementary sections from the base or proximal end of the petiole are sometimes used. As might be expected, the vascular structure is less complex in simple than in compound leaves, but this direct relationship between elaboration of leaf form and complexity of vascular structure is by no means universal.

The principal types of vascular system which can be seen in transverse

sections through the distal ends of dicotyledonous petioles are shown in Fig. 1 A-I. Each type may consist of a single vascular strand or be dissected into a number of bundles according to the species. Types of structure intermediate between those shown in the figures also occur. It should also be remembered that in certain families, such as the Dipterocarpaceae, the petiolar vascular structure is more complex (Fig. 53 A-D). There is also a type of

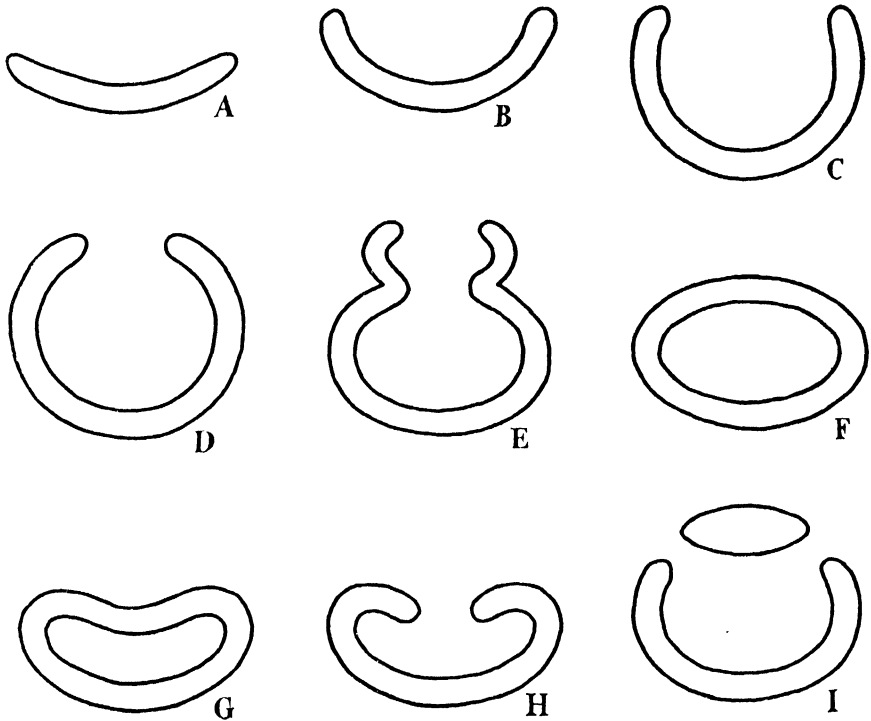


FIG. 1. A-I, Types of vascular structure visible in transverse sections through the distal ends of dicotyledonous petioles. Each type may appear as a single vascular strand or be dissected into a number of bundles in different genera and species.

petiole with scattered bundles, e.g. in *Anemone vitifolia* (Fig. 4 J), and some special types of vascular structure that occur in some species of *Populus* are illustrated (Fig. 3 I4 D and F). It should also be emphasized that the structure of the petiole is very imperfectly known, but such facts as have been recorded suggest very strongly that this field would repay further investigation.

6. MICROCHEMISTRY. (See also under 13 (i) on p. xxviii)

In the course of a broad anatomical survey one cannot fail to be impressed by the many types of chemical deposits which occur in plant tissues. Sometimes these occur in cells which do not differ in appearance from their neighbours or, alternatively, they may be in special secretory structures or elements. The diverse nature of the substances secreted suggests that there must be correspondingly great physiological differences between the plants in which they are exemplified. The author feels that, because the nature of secretory

structures and their contents are intimately bound up with the basic physiological processes of the plants in which they occur, they might be expected to be particularly valuable as indicators of taxonomic affinity. In practice there is good evidence in favour of this suggestion. For example, taking the genus *Senecio* in a broad sense, we find similar secretory structures throughout the various species quite irrespective of their range of habit forms which includes annual herbs, stem- and leaf-succulents, shrubs, and even trees. In spite of this diversity of habit, the secretory system of *Senecio* at once enables the stem-succulent species to be distinguished from similar stem-succulent plants belonging to other families, whilst the task of identifying the herbaceous and arboreal members of the genus is greatly simplified by the restricted number of families in which a similar secretory system is known to occur. The chief types of secretory structures and secretions will now be considered.

(a) *Crystals*. (See also under 13 (i) on p. xxviii)

The most common crystals consist of variously shaped deposits of calcium oxalate. Some types, such as solitary prisms or clusters of various descriptions, are relatively widespread. Nevertheless, even with these relatively widely occurring types, the kind or kinds secreted by any one species appear to be fixed. Where more than one kind is secreted in a particular species the relative proportions of each are frequently found to vary, generally in accordance with the types of nutriment available or with the time of year. Other types of crystalline secretion such as raphides and crystal-sand are more restricted in distribution and therefore of still greater taxonomic interest. Sometimes a whole family is characterized by the secretion of a highly distinctive material. This applies for instance to the Cruciferae where myrosin is very common. Likewise berberin is secreted in the Berberidaceae and to a certain extent in related families such as the Menispermaceae and in certain Ranunculaceae. A word of caution is necessary, however, as there are instances where similar chemical substances are synthesized in quite unrelated families, e.g. coumarin in certain grasses and a few Leguminosae, or rubber in Compositae, Euphorbiaceae, Apocynaceae, and other unrelated families.

(b) *Starch*

The size, shape, and other characters of starch grains, such as their appearance in polarized light, are highly distinctive and consequently of considerable taxonomic value. The botanical origin of commercial starches can be established by their microscopical characters.

(c) *Cystoliths*

The secretion of silica, calcium carbonate, and other chemical substances in the form of relatively large concretions known as cystoliths is highly characteristic of certain families, e.g. Acanthaceae, Urticaceae, &c.

(d) *Laticiferous System*

In certain families there is a well-developed system of tubes or cells in which variously coloured colloidal fluids known as latex are secreted. Laticiferous tubes and cells sometimes occur together in the same plant. The term latex, although convenient, covers a series of fluids of diverse chemical com-

position. Thus the white milky latex of the Para Rubber Tree (*Hevea brasiliensis*) is the chief commercial source of rubber, while the well-known yellow latex of *Chelidonium majus* contains very little. Nevertheless laticiferous elements are of diagnostic value, whatever the precise chemical nature of their contents may be, because of their restricted occurrence and the ease with which they may be seen. Since latex is secreted in quite unrelated families its presence must not in itself be taken as indicative of taxonomic affinity unless this is also supported by other characters.

(e) *Secretory elements*

Besides the laticiferous system, other secretory elements in which oils, resins, mucilage, tanniniferous substances, &c., are deposited are of considerable taxonomic value. These substances are deposited in cells, intercellular cavities, elongated sacs, and canals, the last often being lined with a definite epithelium. The morphology of the secretory elements, their distribution within the plant, and the chemical nature of their contents are often highly distinctive. The nature of the contents has sometimes been assumed rather than demonstrated by actual tests, so that many terms such as 'oil cells', 'resin canals', &c., have frequently been used in a rather loose sense in the literature of plant anatomy. Another reason for this lies in the fact that the deposits in secretory elements are seldom pure substances, so that tests applied by different authors to the same material may lead to various conclusions. Thus we find in the Lauraceae that the familiar, large secretory cells have sometimes been described as 'oil cells', though in some species these contain mucilage and not oil. There appears to be considerable scope for more intensive work on the chemistry of secreted material as an index of taxonomic relationship. If circumstances do not permit a sufficiently comprehensive chemical investigation to be made, the investigator would be well advised to apply descriptive terms to the contents of these elements, rather than to assume their chemical nature and so perpetuate inaccuracies. To describe deposits as being 'solid, red, amorphous' is less misleading than to describe them as 'gum' when they may be chiefly 'resinous' or 'tanniniferous'.

7. CORK

Solereder attached considerable diagnostic importance to the position in which the cork originates in a young stem, and this character is undoubtedly of value within limits. It must be borne in mind that, even in an individual species, the first cork to be formed is often more superficial than that which arises later on. Then again, within a single family there are frequently species with either superficial or deep-seated cork respectively, although in other families the position of origin of the cork appears to be more constant. Solereder further stressed the importance of the exact position in which the cork arises even within the superficial and deep-seated categories. This character, however, does not appear to the author to merit such detailed investigation.

8. ENDODERMIS

The presence of a well-marked endodermis in stems is of diagnostic value because of its restricted occurrence. In most dicotyledonous stems

the endodermis is by no means obvious; in some it consists of a more or less clearly defined layer of cells which differ from their neighbours in containing starch; in a third group the endodermis, in the same way as is normal for the root, consists of cells with well-marked casparian thickenings. In a few species the endodermis becomes wholly suberized.

9. 'PERICYCLIC' SCLERENCHYMA

In the stems of many plants the 'pericycle' is not clearly defined, nor, in fact, is there any general agreement concerning the precise meaning of this term. There is, nevertheless, a portion of the stem between the inner boundary of the primary cortex and the outer part of the primary phloem in which mechanical elements usually arise. These mechanical elements are generally referred to as 'pericyclic'.

The presence or absence and nature of the 'pericyclic' sclerenchyma is easily determined and of taxonomic value. The most common types in transverse sections through an internode are: (i) An interrupted ring of fibres. (ii) A continuous ring of fibres. (iii) An interrupted ring of mixed fibres and stone cells. (iv) A continuous ring of mixed fibres and stone cells, which is commonly described as 'a composite, continuous ring of sclerenchyma'. (v) Stone cells present, but no fibres. (vi) Sclerenchymatous elements entirely lacking. More than one of these arrangements is frequently to be seen in a single species, especially in stems of different ages. In particular a sclerenchymatous ring may be continuous or interrupted at different stages of its development. For this reason it is desirable when comparing the 'pericyclic' sclerenchyma in two specimens to ensure that the sections are taken through internodes of the same age.

The amount of sclerenchyma in the 'pericycle' does not necessarily depend on whether a plant is woody or herbaceous. For example, a well-defined ring of fibres occurs in herbaceous species of *Linum*, whereas there are only isolated strands of fibres in certain shrubs, such as species of *Forsythia*. On the other hand, 'pericyclic' sclerenchyma is particularly well developed in the Beech (*Fagus sylvatica*), but very little is developed in the herbaceous *Lamium album* and it rarely occurs at all in the Umbelliferae.

The nature of 'pericyclic' sclerenchyma is helpful in separating species or genera in some families, but in a few instances the arrangement may be typical of a whole family, e.g. 'pericyclic' sclerenchyma is typically absent from all investigated members of the Pittosporaceae, whilst a sclerenchymatous ring of a very characteristic type occurs throughout the Geraniaceae.

10. WIDTH OF MEDULLARY RAYS

In the internodes of young stems of many plants the primary vascular bundles appear to be widely separated from one another by parenchymatous tissues which may be regarded as constituting very broad medullary rays, e.g. in the herbaceous Ranunculaceae. In extreme cases the vascular bundles are scattered, or show a tendency to be scattered, in the same way as those of Monocotyledons, e.g. in Piperaceae, herbaceous Berberidaceae, &c. In transverse sections through the internodes of other plants, however, the xylem appears as a closed ring, traversed by very narrow medullary rays. In these plants the primary bundles are not individually distinct, e.g. in the Theaceae.

Other plants exhibit an intermediate structure. These different kinds of arrangement have not received, from the taxonomist, all the attention they appear to merit, presumably in the mistaken belief that they are chiefly expressions of habit differences, a continuous ring of xylem having been regarded as typical of woody plants, and separate bundles as typical of herbs. If this were entirely true little or no taxonomic significance could be attached to these differences. As will be seen from the descriptions of the families in this book, however, there are woody plants like *Clematis* and *Menispermum* in which the primary bundles are separated by broad medullary rays; on the other hand, the herbaceous Linaceae and the tribe Galieae amongst the Rubiaceae have a continuous ring of xylem, whilst in *Veronica* even the most slender herbs are devoid of medullary rays. Solereder states that the diversity of arrangement of the vascular system of herbs is so varied that it is of little practical taxonomic value, and he pays but little attention to the subject. Experience suggests, however, that the primary vascular structure is probably of greater taxonomic significance than many of the features that Solereder emphasized. Much new information on this subject is incorporated in this book.

11. BICOLLATERAL BUNDLES

The habitual occurrence of bicollateral vascular bundles in the axis of a family, e.g. the Cucurbitaceae, is often a useful diagnostic character.

12. CORTICAL AND MEDULLARY BUNDLES, AND ANOMALOUS SECONDARY THICKENING

All of these features are of diagnostic value on account of their restricted occurrence, but the families in which they are to be found are seldom closely related to one another.

13. WOOD. (See also pp. xl-li)

The structure of the xylem in the young twigs of shrubs and trees often differs in certain respects from that of the mature trunk. Solereder's remarks concerning the wood were often based on features seen in twigs taken from herbarium sheets and, being, therefore, not typical of the mature wood, are of doubtful value for the identification of commercial timbers. In a young twig the dimensions of the cells, both diameter and length, are markedly smaller than in the mature wood, there often being an increase of 100 per cent. over those of the first ring; in addition the distribution of the vessels, the occurrence and arrangement of the parenchyma, and even the nature of the fibres that form the ground-tissue of the xylem may be unlike those of the mature wood. It is not unusual to find vessels with scalariform perforation plates in the young wood of a species which has exclusively simple perforations in the mature wood, or heterogeneous rays in the first rings changing later to homogeneous rays.

On the whole the wood structure appears to possess features that are more conservative than those of the external morphology, and in consequence specific differences are often less clearly expressed in the wood than in the external features. Many microscopical characters of the wood are also less plastic than both the exomorphic features and many anatomical characters of

other parts of the plant body such as the leaf; this, combined with its more conservative nature, adds to its value for the study of larger groups. There are, however, some characters, such as the number and size of the vessels and the amount of parenchyma present, that may be markedly influenced by the environment, and these features are relatively unimportant for taxonomic purposes.

The characters of the wood that have been found by experience to have the greatest taxonomic value are discussed below (see also p. xl).

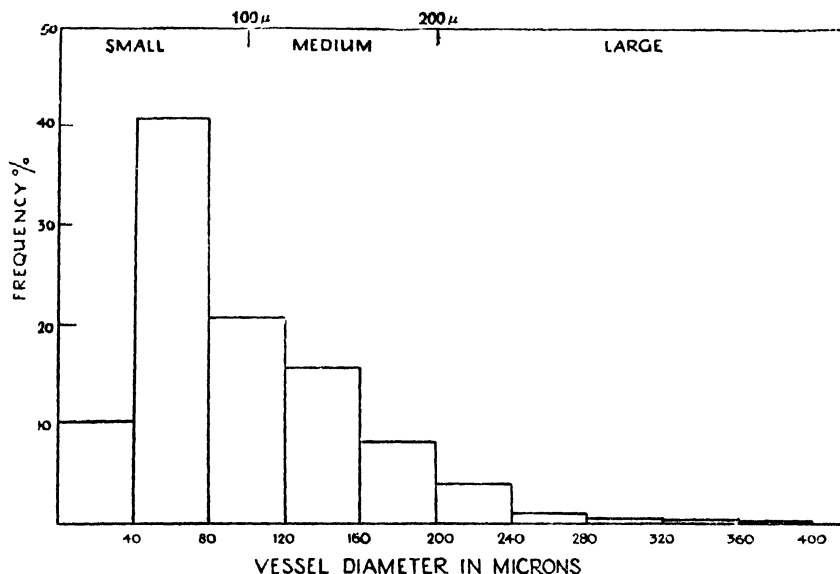


DIAGRAM I. Distribution of Mean Vessel Diameter in the Dicotyledons.

(a) *Vessels*

The most useful characters are distribution, pattern, diameter, and frequency as seen in transverse sections, type of perforation, pitting between one vessel and another (intervascular) and between vessels and wood- or ray-parenchyma cells, and the occurrence of spiral thickening. The presence of tyloses may be of value, but it is sometimes doubtful if their formation is a constant feature and they are normally lacking from sapwood. Where tyloses are pitted, contain crystals, or have a characteristic shape, as in the Sapotaceae, they have a greater diagnostic value. Vessel diameter is best recorded as a mean figure; though varying according to position in the tree and conditions of growth, it is often of considerable value for identification, as it may differ markedly in closely related woods. It is not practicable to use mean vessel diameter for a ring-porous wood. The range of mean diameters in the Dicotyledons is shown in the above histogram, which is based on 1,500 species (see also Appendix I, Table 1, on p. 1360). Vessels are described as 'small' if their mean diameter is less than 100μ and 'large' if it is more than 200μ .

The number of vessels per sq. mm., though useful, is difficult to determine. In many cases it is extremely difficult to distinguish the smallest vessels of a

group as seen in transverse section from tracheids or fibre-tracheids, and a convention has been commonly adopted to treat all the vessels of a group as a single unit when making counts. The figures obtained in this way (see Appendix I, Table 3) do not conform to any normal distribution curve. The range is very great, from fewer than 1 per sq. mm. to over 300. Very low or very high figures tend to be characteristic of some families. For example, most of the woods of the Caesalpiniaceae, Papilionaceae, and Rosaceae-Chrysobalanoideae have fewer than 5 vessels per sq. mm., whereas the woods of the other Rosaceae typically have more than 40 per sq. mm.

Vessel member length is seldom used for identifying timbers. It can only be measured satisfactorily in macerated material and should consist of the total length (359). It must be emphasized that vessel member length, in common with other cell dimensions, varies considerably within any species and even in different parts of the same tree. Bailey and Tupper (100), for example, have shown that the first-formed members are shorter than those developed later, that slow-growing plants often have shorter members than fast-growing and that, within the same species, dwarf plants tend to have shorter members than normal individuals. Nevertheless, vessel member length is of very great importance for phylogenetic studies, and the distribution of mean length throughout the Dicotyledons is shown in the following histogram, which is based on 600 species (see also Appendix I, Table 2, on p. 1360). Vessel members whose mean length is less than 350μ are described as short, and those over 800μ as long.

(b) *Wood Parenchyma*

The distinction between the main types depends on the distribution as seen in transverse sections. There has been, and still is, considerable difference of opinion concerning both the types to be distinguished and the terms that should be applied to them. It is therefore desirable to describe here the meaning of the terms used later in the descriptions of the families.

The scheme adopted is a combination of the terms given by the International Association of Wood Anatomists in its Glossary (1119) and the subsequent modifications suggested by Kribs (1287), Bailey and Howard (83), and Chalk (354). For the benefit of readers who are not specialists in wood anatomy, the parenchyma has usually been described in the text as well as labelled, as, for example, 'Parenchyma scattered as isolated cells among the fibres (diffuse)'.

A basic distinction is drawn between 'apotracheal' types, in which the distribution is fundamentally independent of the vessels, and 'paratracheal' types, whose distribution is determined primarily by the vessels. Apotracheal types may often touch some or all of the vessels, particularly where either the vessels or the parenchyma are abundant, but such contacts are, so to speak, accidental. Three main types of apotracheal parenchyma are distinguished—terminal, diffuse, and metatracheal. Terminal parenchyma occurs between the end of one growth ring and the beginning of another, either as scattered cells or, more commonly, as a continuous band (Plate A, 1). The name 'terminal' has been shown by Chowdhury (412, 413) to be in some instances a misnomer, as the parenchyma band may be the first-formed tissue of the new ring and not the last-formed tissue of the old. For this type he has proposed

the term 'initial', but, as it is not practicable to make this distinction on the ordinary wood sample, the term has not been used in this work, except where it is recorded in the literature.

Of the other apotracheal forms there is a complete series from 'diffuse', with isolated cells scattered among the fibres (Plate A, 2), to regular, continuous 'metatracheal' bands (Plate A, 5-7). Bailey suggests that the term 'metatracheal' should be dropped, owing to the different senses in which it has been used, in favour of 'banded'. The intermediate forms present some difficulty, particularly where the cells tend to be grouped into short lines from

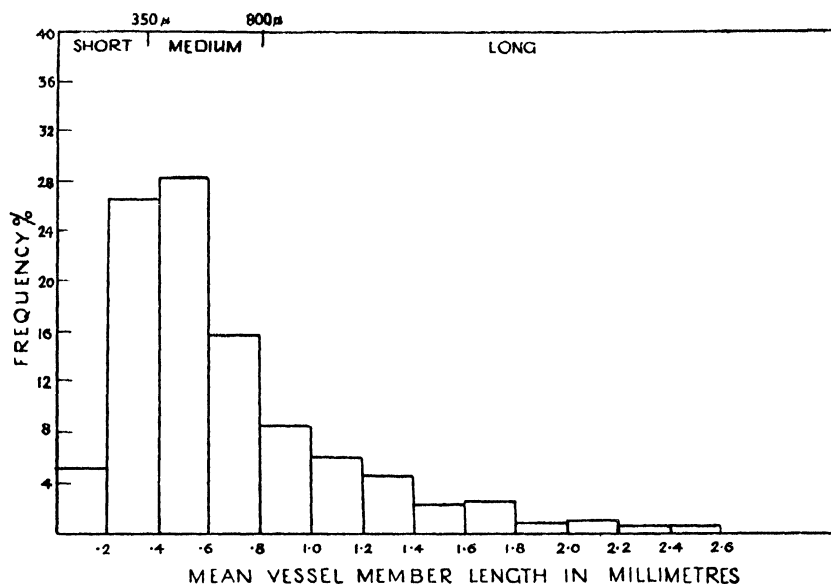


DIAGRAM II. Distribution of Vessel Member Length.

ray to ray (Plate A, 3 and 4). These are sometimes classed with the isolated cells under the term diffuse, but there is much to recommend the use of a separate term, such as 'diffuse-aggregate' or 'diffuse-in-aggregates', as suggested by Kribs and Bailey respectively. In the text this type has usually been described in some such terms as 'scattered among the fibres as isolated cells and short uniseriate lines'.

The term 'reticulate' is applied to banded types in which the parenchyma bands are similar to the rays in width and spacing, so that the two together give the appearance of a net, as in Plate A, 3 and 6.

Various forms of paratracheal parenchyma are illustrated in Plate B. The three main types are 'vasicentric' (B, 3), a sheath concentric with the vessel, 'aliform' (B, 4), a sheath projecting from the sides, and 'confluent' (B, 6), the parenchyma round some of the vessels linking up to form bands. There has been some difference of opinion concerning whether a few cells round the vessels (not forming a complete sheath) should be included under the term vasicentric. Kribs suggested the phrase 'scanty vasicentric', which Bailey amended to 'scanty paratracheal', and the latter has been used in the text (see

Plate B, 1). Another useful term suggested by Bailey and adopted here is 'abaxial', to describe forms in which the parenchyma is limited to the side of the vessel farthest away from the pith and often extends from the vessel as lateral wings (Plate B, 2). Kribs has also used the term 'banded paratracheal'.

An entirely different parenchyma feature, which has been described in the text, and which may need a brief explanation, is the number of cells in a parenchyma strand or longitudinal file of cells formed from a single cambial initial. Most commonly of four cells, the number may be up to as many as sixteen in woods with long cambial initials, and in many short strands there may often be a single cross-wall or none. The latter strands, each consisting of a single cell, are now known as fusiform parenchyma cells; in the older literature they are referred to as substitute or intermediate wood fibres.

(c) Rays

The most widely used character of the rays is width, either in actual dimensions or in number of cells; height is also of value, but usually only in extremes, when very high or very low. 'Rays exclusively uniseriate' is another feature of great value for identification, particularly as it represents a type of structure that occurs rather sporadically, and may thus offer a distinction between closely related genera or species, e.g. between particular species of *Guarea* and *Terminalia*. Other useful characters are the various types of heterogeneous and homogeneous rays (Plate C), tile¹ cells and oil or mucilage cells. The frequency of rays is often a useful character. It is usually measured by counting the rays along a line at right angles to the rays on either a transverse or tangential section, and is expressed as the number per millimetre. The number is sometimes characteristically high or low in particular families, numerous rays being, for example, typical of the Myrtaceae and Rubiaceae. The distribution of ray number in the Dicotyledons is shown in the following histogram, which is based on 1,800 species (see also Appendix I, Table 6).

Ray width, though theoretically best expressed as a mean value, is so much more easily measured as a maximum that it is usually given in this form. The distribution of maximum ray width in the Dicotyledons is shown in the histogram, which is based on 650 species, in Diagram IV (see also Appendix I, Table 5). Rays whose maximum width is less than 50 μ are described as fine and those over 100 μ as broad.

(d) Fibres

It is usual to distinguish between 'libriform fibres' with simple pits, and 'fibre-tracheids' with bordered pits, but no exact definition of these two types appears to be universally acceptable. Intermediates are so numerous that it was found more satisfactory in the text to group all types under the single heading 'Fibres'. The most important characters of fibres are the nature of the pitting and the presence or absence of septa. Of particular interest are instances where septate fibres are grouped together in a manner suggestive of parenchyma, as in many of the species of the Celastraceae. Fibre length,

¹ Tile cells have been defined (1119) as a 'special type of apparently empty upright or square cells of approximately the same height as the procumbent cells and occurring in indeterminate horizontal series usually interspersed among the procumbent cells. (Common in certain of the Tiliales and Malvales)', and are described and illustrated by Chattaway (371).

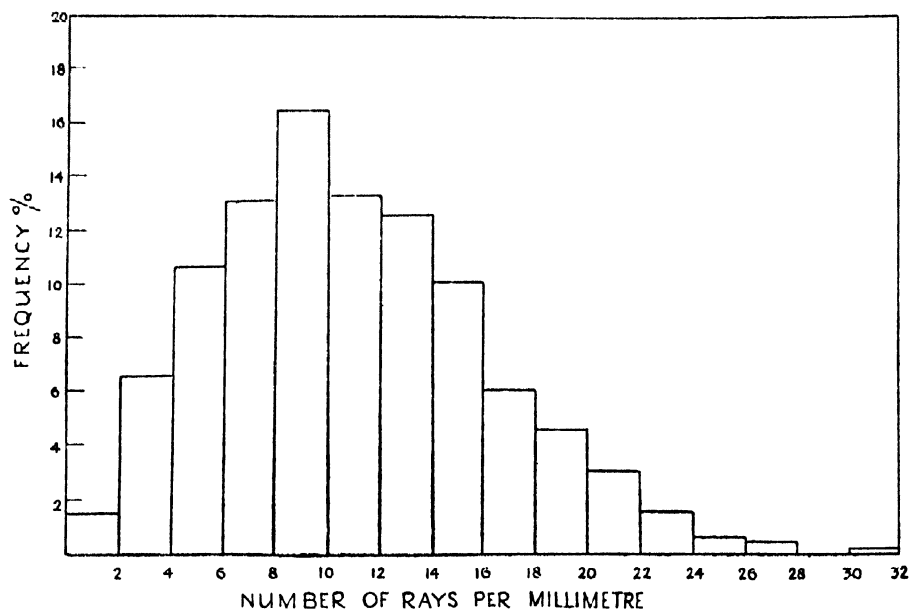


DIAGRAM III. Distribution of Ray Number.

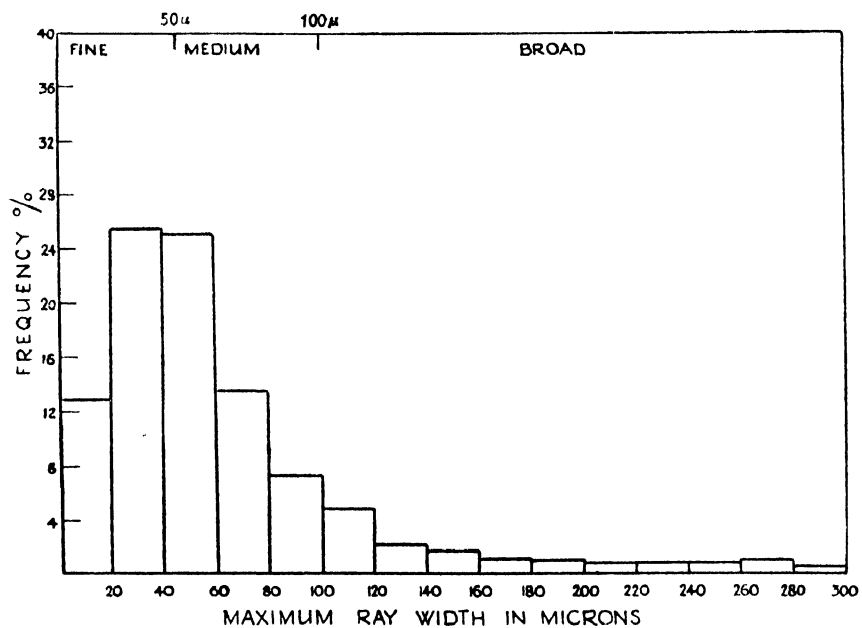


DIAGRAM IV. Distribution of Maximum Ray Width.

though little used for diagnostic purposes, is of some practical interest and has been included in the text. The distribution of mean fibre length in the Dicotyledons is given in the following histogram, which is based on 534 species (see also Appendix I, Table 4). Fibres whose mean length is less than $900\ \mu$ are described as short, and those over $1,600\ \mu$ as long.

(e) *Storied Structure*

This is a most useful character. It consists of the arrangement of the cells or tissues in horizontal series as seen in tangential section (see Fig. 117 D).

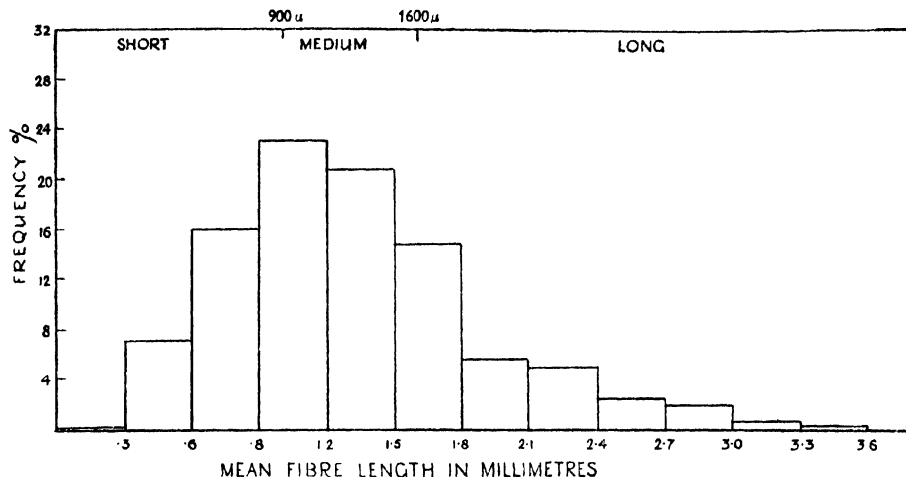


DIAGRAM V. Distribution of Mean Fibre Length.

In some cases only the rays are storied, or grouped in horizontal series like the windows of a house; in others all the elements are storied; in others, again, only the wood parenchyma. Storied structure has been described in the text under each element or tissue in which it occurs. A list of the families in which the feature occurs is given on p. 1352.

(f) *Growth rings*

Although this character is a standard feature of most descriptions of species, it was omitted from the present work because it was found that so little useful information could be added to a family description under this heading. The heading has, however, been retained to record any investigations on cambial activity and the development of the tissues. Any special points connected with the growth ring, such as terminal parenchyma, markedly thicker-walled fibres at the end of the ring, &c., have been recorded under the type of cell concerned.

(g) *Included (Interxylary) Phloem*

This form of anomalous structure has been recorded, where appropriate, under the description of the wood. A list of the families in which it occurs is given on p. 1352. The terminology adopted is that given by Pfeiffer (1712) and used also by Chalk and Chattaway (362).

(h) *Intercellular Canals* (see also under 6 (e) on p. xix)

Both the vertical and radial types are of great diagnostic value. Lists of the families in which they occur are given on pp. 1353-4. Latex tubes, which sometimes occur in the rays, are also of value, but are rare.

(i) *Deposits and Chemical Reactions* (see also under 6 (e) on p. xix)

The presence of deposits of unusual substances may be of great value where facilities are available for identifying them, and such facts as are recorded in the literature and appear likely to be of taxonomic use have been included in the text. Otherwise, observations have been limited to the visible aspects of deposits, such as colour and whether crystalline or gum-like, and the terms 'gum-like' and 'gummy' have been used without any chemical significance. The degree of lignification of the cell wall, as indicated by stains, has sometimes been referred to, particularly the occurrence of a mucilaginous layer in the wall of the fibre or areas of tissue with unlignified cell walls.

GENERAL CONCLUSIONS

If one surveys the Dicotyledons as a whole, the anatomical evidence confirms that some families are relatively homogeneous and therefore probably natural, while others are seen to be heterogeneous and therefore in need of revision or at least reinvestigation. So far as the constitution of families is concerned, anatomy points to the desirability of local amendments rather than complete reorganization. For example, a genus may be shown to need transferring to another family or possibly to form the basis of a new one, or the dividing line between closely related families may need modification. Examples will also be found in this book of groups of families that have sufficient anatomical similarity to justify the conclusion that they constitute larger natural groups or orders, e.g. the Malvales. Other orders seem to be more artificial, with little in common between their constituent members, in which case it is better to recognize that the families are isolated than to try to force them into a group. Every family must obviously be included somewhere in a flora, but, where affinities are doubtful, this should be clearly indicated. Modern angiosperms represent only the existing end-points in an evolutionary process of which the early course is almost unknown, and previously existing groups may have become extinct without leaving any known record for our guidance. When, in addition, one must acknowledge that the very origin of the angiosperms is a matter of conjecture, the difficulties in the way of making a truly natural classification will be seen to be very great. It is therefore important that any attempt to do so should neglect no evidence and should be based on as many attributes as possible; two of the most important of these are external morphology and microscopic anatomy.

Limitation to woody stems obviously reduces the general taxonomic value of wood anatomy, but that it can be of great value in particular groups is now generally recognized. It must be emphasized again, however, that the evidence from wood anatomy needs careful interpretation, particularly in order to distinguish between characters, such as type of perforation and intervacular pitting, that are associated primarily with level of specialization and those that are likely to indicate affinity.

This section may be appropriately ended by a quotation from T. A. Sprague (2172):

'It should be clear that future progress in the classification of the groups of higher rank will be by synthetic methods—not by attempting to make a complete scheme embracing every family, but by placing such families together as show maximum correlation of characters, and by building up larger groups from them. A natural classification built up in this way will for many years be very incomplete, but it will have the supreme merit of being based on established facts instead of individual opinions.'

Selected Literature. (See also p. lxii)

Anderson 26, Bailey 71, Bandulska 129-32, Bartlett 145, Camp 332, Campbell 335, Fritsch 723, Greenman 813, Gunderson 846, Heinsch and Wetmore 939, Hill 970, Hutchinson 1113, Metcalfe 1500-2, Netolitzky 1588, Odell 1628, Rusby 1968, Seward 2081A, Sherff 2088, Sprague 2172, 2172A, Stopes 2208, Stopes and Fujii 2209, Tippo 2263, Turrill 2303, 2304, Watson 2368, Weiss 2392, Wettstein 2416.

ANATOMY AND PHYLOGENY

It is a familiar fact that very little is known about the ancestry of the flowering plants, owing to the imperfect geological record. For this reason most of the views which have been expressed concerning angiosperm phylogeny rest mainly on facts of comparative morphology tempered by a generous seasoning of speculation. Taxonomists and morphologists, stimulated by the classical writings on evolution during the last century, have sought for characters which may respectively be regarded as primitive or advanced from the evolutionary standpoint. Series of characters which are believed to possess these attributes in varying degrees have been found, and, by making use of them, the families of flowering plants have been arranged by systematists in branched, linear series that are commonly treated as if they represent phylogenetic trends along which evolution may be assumed to have progressed. The result has been the various systems of classification which are well known to taxonomists. These systems are all much alike so far as the composition of families and taxonomic units of lower rank are concerned. It is true that there are differences concerning the lines separating closely related families, that there is lack of agreement concerning the advisability of raising certain genera or groups of genera to the status of families, and that opinions differ concerning the true affinities of certain genera. Further investigation is, however, gradually leading to a more general agreement concerning those matters which are still unsettled. Nevertheless the fact that there is such a large measure of agreement common to all reliable taxonomic systems is in itself very remarkable, and tends to show that modern taxonomy rests on a firm basis of well-established facts.

When we turn to taxonomic units above the rank of families, it is at once apparent that there is no general agreement concerning their composition. The differences of opinion are still greater when we pass from the purely taxonomic realm into that of phylogeny. One of the chief reasons for this lies in the fact that there has been much speculation concerning the phylogeny of the existing plant families. The reliability of a phylogenetic system is largely

a measure of the knowledge and wisdom of its author, and all views which have been expressed concerning the phylogenetic interrelationships of plant families are largely a matter of personal opinion. To the author, as indeed to many other botanists, it appears highly improbable that the families of flowering plants as we know them to-day have been evolved from one another. Those that agree with each other taxonomically in many respects may well have had a common ancestry, but it seems fundamentally misleading to arrange them in a single, linear, phylogenetic series even if this has the form of a *branched* tree. It is surely more profitable to recognize that the families and taxonomic groups of lower rank represent the present levels which have been reached by plants that have evolved along lines of descent between which there has been no direct connexions except possibly in a remote geological age. Even then there can have been a direct connexion between them only if all of the modern flowering plants have been derived from a common pre-angiospermic stock. That this was so has yet to be proved by irrefutable evidence.

It is well known to students of palaeobotany that one of the greatest evolutionary problems is how the flowering plants originated, and from what pre-angiospermic stock they made their sudden appearance in the Cretaceous era. The palaeobotanical record from the Cretaceous deposits of Greenland affords evidence of the contemporary existence of forests of plants resembling modern plane trees, as well as of species which can be identified as having affinities with such wholly unrelated modern genera as *Artocarpus*, *Cinnamomum*, *Dalbergia*, *Magnolia*, *Menispermum*, and *Quercus*. In the Cretaceous of Colorado and New Mexico the remains of palm-like plants, and of species which recall the modern genera *Ficus*, *Juglans*, and *Quercus*, have been found. In the late Cretaceous, in addition to the plants already mentioned, genera allied to *Salix*, *Myrica*, *Bauhinia*, *Sterculia*, and *Eucalyptus* are known to have occurred. In view of the coexistence of such diverse types amongst the earliest known fossil angiosperms one cannot, in the absence of a more exact geological record, decide which of them is more primitive than others. There is no fundamental reason why they should not have been evolved from different pre-angiospermic stocks. In fact this seems no more improbable than that the origin of the angiosperms was a solitary evolutionary event.

Because of the paucity of geological evidence, taxonomists make use of comparative morphology when attempting to elucidate phylogenetic sequences. In this connexion series of morphogenetic progressions have been proposed which demonstrate possible lines along which relatively advanced plants may have been evolved from simpler forms. Floral examples are afforded by the changes from polypetaly to gamopetaly, from radial to bilateral symmetry, from the superior to the inferior gynoecium, or from the atropous to anatropous position of the ovule. Others are also recognized, and further details may be found in Sprague's (2172A) paper. Morphogenetic progressions such as these have not yet been proved to represent actual evolutionary sequences, but it is more reasonable to assume that changes have taken place in the directions indicated rather than in the reverse. If it be accepted that this line of reasoning is legitimate, it can at once be seen that there are families of Dicotyledons, such as the Papilionaceae and Compositae, which may be regarded as relatively advanced and others, such as the Ranunculaceae, which are relatively primitive.

In the same way it is possible within a family to recognize relatively primitive and advanced genera and species. We thus obtain a glimpse of possible modes of evolution within the angiosperms, but the mere fact that such sequences probably occurred must not be taken to mean that any existing families have necessarily been evolved from one another directly.

During the past fifty years, the problem of angiosperm phylogeny has also been approached by anatomists working along several distinct lines. The early investigations were concerned with stelar structure, followed by a period devoted to studies of the relationship between the arboreal and herbaceous habits, whilst more recent phylogenetic work has dealt with nodal anatomy and wood structure. Each of these lines of inquiry will now be considered in more detail. →

Stelar structure

At the beginning of the present century, speculation concerning the origin of the angiosperms led to frequent comparison being made between their vascular anatomy and that of plants from which they might have been derived. It was commonly held that the primitive vascular system of the axis was a protostele, in which a solid central cylinder of xylem was surrounded by phloem and an endodermis (Fig. 2 A). This type of structure persists in modern plants amongst some of the ferns and lycopods, whilst other Pteridophytes, which possess a more complex vascular system when mature, nevertheless exhibit a protostelic structure when the sporophyte is still young.

The protostele is still generally held to be the ancestral to other types of vascular structure, but there has been speculation concerning the manner in which the transitional stages were effected. From the point of view of the prehistory of the angiosperms the most essential conception is that the central portion of the protostele became medullated or converted to parenchyma. According to one view this change may have occurred by the intrusion of the parenchyma of the cortex through gaps in the protostele associated with the departure of vascular strands to supply the leaf. By others it was held that the conversion of the central tissues of the protostele to parenchyma was a direct process in which intrusion of parenchyma through leaf gaps was of no significance. Whichever of these alternatives represents the actual course of events, the important point is that a tubular vascular system was formed as a result, and this was termed a medullated protostele or siphonostele (Fig. 2 B) and represents the basic structure of many angiosperms at the present day. A variant of the continuous siphonostele was one in which the xylem and phloem became dissected so as to give a ring of separate vascular strands each consisting of xylem and phloem (Fig. 2 C). This polyfascicular type of stele occurs in many angiosperms at the present day, and, as indicated below, there has been considerable controversy concerning the mode of transition from the continuous to the dissected type. Some botanists have held that this change was effected by the devascularization of tissues opposite leaf-traces, whilst others believe that it took place by the reduction or suppression of cambial activity accompanied by enlargement of primary rays, without the leaf-traces having taken any important part in the process. Another variant of the siphonostele is to be seen in Fig. 2 F. This differs from the structure shown in Fig. 2 B in having a layer of phloem on the inside as well as on the

outside of the xylem. This type of structure is to be seen amongst the Pteridophyta in such plants as *Marsilea* and *Loxsonia*, whilst amongst the angiosperms it is represented by families possessing internal phloem, e.g. *Solanaceae* or *Asclepiadaceae*. Other variations of the medullated protostele and siphonostele also occur depending on the extent to which the phloem and endodermis extend into the interior of the xylem cylinder through the leaf gaps and also on the extent to which the external phloem has the form of a

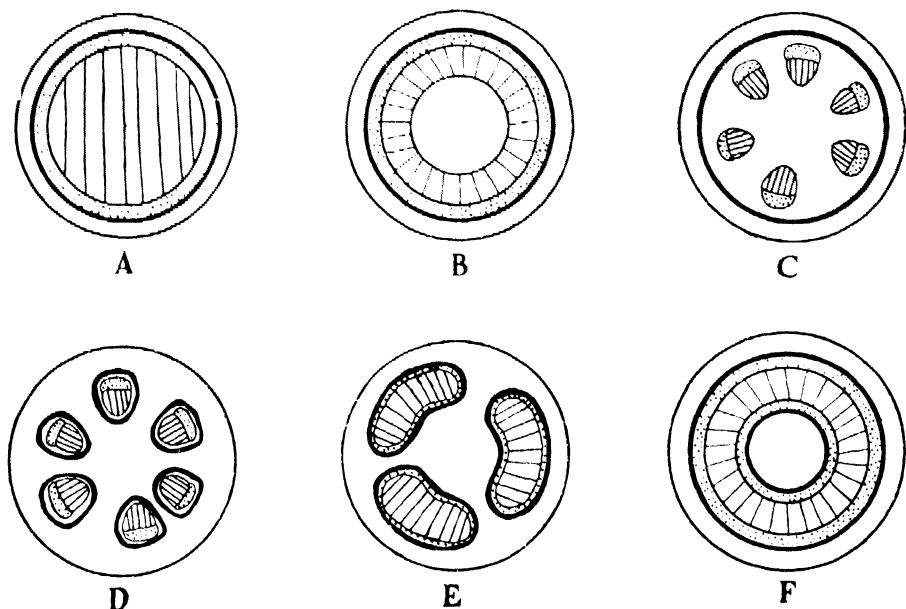


FIG. 2. A, Protostele. B, Medullated protostele or siphonostele. Type I. C, Medullated protostele, Type II. D, Astelic, e.g. as in *Nymphaea*. E, Polystelic, e.g. as in *Pteridium aquilinum* (L.) Kuhn and certain species of *Primula*. F, Medullated monostele with internal phloem and endodermis, e.g. as in *Marsilea* or *Loxsonia*. The thick black lines adjoining the phloem represent endodermis. For further details see p. xxxi.

continuous or dissected cylinder. These are not, however, important in the present discussion, so it will suffice merely to note their existence. If, when the siphonostele is dissected, each vascular strand becomes completely enclosed by an endodermis, the resulting structure is a polystele (Fig. 2 D, E) which occurs amongst advanced ferns such as the common Bracken (*Pteridium aquilinum*) and in certain of the *Auricula* section of the genus *Primula*. These various types of stelar structure and their interrelationships have been more fully described by T. G. Hill (974). ✓

Herbs and Trees

During the period from 1911 to 1922 there were many investigations and much speculation concerning the phylogenetic relationship of the arboreal and herbaceous habits in the angiosperms. The botanists mainly concerned were Bailey, Eames, Jeffrey, Sinnott, Thompson, and Torrey, whilst the leading American and British botanical journals of that period abound with articles on the subject. After a lapse of several years Arber (30) took up the

subject again, but even at the present time it seems improbable that the last word has been said.

At the beginning of this period it was generally believed that, in the internodes of typical herbaceous stems, there is a ring of collateral vascular bundles separated from one another by relatively broad areas of parenchymatous tissue. This arrangement was also thought to exist in the young stems of shrubs and trees, whilst, in the more woody plants, the cambium, instead of remaining confined to the vascular bundles as in the herbs, became converted to a continuous ring by the development of a zone of meristematic tissue across the parenchyma between the bundles. There was thus a distinction between the cambium of the primary bundles which was termed fascicular and that which developed between the bundles and was described as interfascicular. By the activity of the interfascicular cambium the original bundles became united to form a continuous ring interrupted only by medullary rays whose width varied considerably in different kinds of plants. This mode of development, which had become familiar through the teachings of Sachs, de Bary, and other botanists in the previous century, doubtless occurs in many plants. It is now known, however, that in other and very numerous species a continuous zone of cambium arises at a very short distance behind the stem apex, so that the distinction between fascicular and interfascicular cambium breaks down.

All of the botanists who were interested in the phylogenetic relationship of herbs to trees during the 1911 to 1922 period probably believed the arboreal habit to have been primitive and the herbaceous habit derived or advanced. This commonly accepted view depends mainly on the well-known fact that the immediate precursors of the angiosperms, together with the early angiosperms themselves revealed in the geological record, were known to have been trees or at least woody plants. It was often forgotten, however, that the geological record is certainly very imperfect, and, while we have no definite knowledge of them, it is at least possible that herbs may have coexisted with the arboreal types. The fact that they have not yet been discovered may be because they were less readily preserved than trees or they may have been comparatively rare. The question of climate was also taken into consideration, especially by Bailey and Sinnott, who pointed out that, in the present era, trees constitute the dominant vegetation of the tropics whilst herbs become progressively more numerous in cooler climes. Since it is generally believed that a warmer climate occurred over a much greater part of the world at the time when the angiosperms first made their appearance than now, it seems reasonable to suppose that arboreal plants may then have been more widely distributed than at present. Bailey and Sinnott regarded the development of a colder climate in the temperate zones, particularly in the Tertiary era, as having played a fundamental part in producing herbs by the reduction of more woody forms. An additional argument, which has frequently been put forward in favour of the arboreal ancestry of the angiosperms, is the familiar one that in other groups of plants below the angiosperms, arboreal forms, now extinct, have been succeeded by herbs which persist until the present day. Here again herbaceous forms may have previously existed beside their arboreal relatives, without their remains having yet been discovered. .

In order to give an anatomical explanation of the phylogenetic transformation of trees to herbs a hypothesis was put forward by Eames (620), and later

elaborated by Jeffrey and his co-workers. This assumed the primitive cauline vascular system of the angiosperms to have had the form of a cylinder of xylem surrounding a central pith, that it was in fact a-medullated protostele. This cylinder became interrupted by parenchymatous tissue above the point of attachment of the leaf-traces to the stem, the necessity for this parenchyma being attributed to the need for storing food near the leaves in which it is synthesized. By the upward and downward extension of the parenchymatous tissue above and below the leaf insertions, and by the simultaneous thinning of the woody cylinder the latter became dissected. If, as the holders of this view believed, the leaf gaps overlapped, it is clear that the primitive vascular cylinder would become converted into a series of distinct fibro-vascular bundles as seen in transverse sections, and in this way the so-called typical herbaceous structure was stated to have arisen. In support of this view the results of anatomical comparisons between herbaceous and woody species were presented in which the facts appeared to be consistent with the theory. It is important to note, however, that most of these comparative studies were limited to a few families, particularly the Compositae.

Eames's and Jeffrey's view that the primitive cauline vascular system had the form of a closed cylinder was strongly disputed by Petersen (1706). Petersen pointed out that there is no evidence to show that plants with a vascular system which appears in transverse sections as a ring of individually distinct vascular bundles is less primitive than the continuous xylem cylinder. She emphasized that plants with widely spaced bundles may have existed beside those with a closed xylem cylinder from the earliest times, so that there is no necessity for regarding the one type of structure as derived from the other. She also observed that even plants like herbaceous species of *Linum*, where a continuous xylem ring is formed whilst the stem is still very young, nevertheless pass through a very brief phase in which independent vascular bundles can be recognized.

Jeffrey and his associates also used another line of argument in support of their views. This is based on what they believed to have been the sequence of morphological changes through which the medullary rays passed during their phylogeny. Jeffrey and his followers regarded the narrow, uniseriate ray as primitive, whilst the so-called 'aggregate' rays in *Carpinus* and other amentiferous trees were believed to represent congeries of narrow or uniseriate primitive rays which became closely associated in the region of leaf-traces. Since many botanists then held, and it is still commonly believed, that the Amentiferae are primitive plants, it was argued that the aggregate ray was a primitive character which still persists. By the subsequent fusion of the components of the aggregate ray and their complete conversion to parenchyma it was believed that the broad 'compound' ray such as occurs in the oaks was formed. As an argument in favour of this view it was pointed out that in certain seedling oaks the broad compound ray does not exist, whilst by traumatic disturbance of mature oaks reversion to the aggregate ray could be induced. The validity of this argument rests on the supposition that characters in a seedling which do not persist in the adult are relics of the type of structure which occurred in mature members in the phylogenetic precursors of the modern species. Furthermore that traumatically induced anatomical changes necessarily represent reversions to an ancestral type. Whilst there

may be some support for both of these ideas, it is improbable that either thesis would command the universal support of present-day botanists. But the difficulties do not end at this point, for it is still necessary to explain the occurrence of narrow rays in the amentiferous Salicaceae as well as in a great range of other angiosperms including many which are generally regarded as advanced types. Jeffrey and his followers appear to have appreciated this difficulty, but they attempted to overcome it by making the rather improbable suggestion that the aggregate ray, besides developing phylogenetically into the broad compound ray in the manner just described, also became split up into progressively narrower components.

Thompson (2253) was one of the first to record evidence which he believed to demonstrate that ancestral rays of the compound type have become narrower by disintegration in certain of the Ericaceae, Casuarinaceae, Betulaceae, and Fagaceae, and this theme was developed by Bailey and Sinnott (97). The disintegration of rays in advanced members of the Betulaceae was also described by Hoar (981). More recent research (138, 1286) suggests that the aggregate ray is a highly specialized structure which occurs sporadically throughout the Dicotyledons, and it is now generally believed that the most primitive ray type is a combination of multiseriate and uniseriate rays, and that woods with wholly uniseriate rays have been derived phylogenetically by elimination of the multiseriates (p. xliii). Ontogenetic dissection of large rays commonly leads to an increase, not a decrease, in their number owing to the subsequent growth of the smaller units.

Bailey (67) appears at first to have been not unfavourably disposed to the concept of the primitive continuous stele having been dissected by parenchyma associated with outgoing leaf-traces. A year later (68), when referring to the modern Fagales, he speaks of the primitive aggregate ray having been reduced and disintegrated in some species and compounded to form the broad multiseriate type in others. Thus *Castanea* and *Castanopsis* with uniseriate rays are regarded as reduced members of the oak family since *Quercus* is characterized by broad rays. In the same way species of *Alnus* which possess only uniseriate and no aggregate rays were regarded as derived from species in which the aggregate rays previously existed. The broad rays of *Quercus* were thought to have been formed by the compounding of previously existing aggregate rays.

By 1914, however, Bailey had been collaborating with Sinnott (97), and in the joint publications of these authors in that year a somewhat different point of view is presented. Bailey and Sinnott agree with Jeffrey and his followers in regarding the herbs as being derived from trees, but differ in their views concerning the method by which this has been accomplished. They rightly regard the fundamental difference between herbaceous and woody plants as consisting of a reduction in cambial activity, accompanied, in some but by no means all instances, by an expansion of interfascicular parenchyma or primary medullary rays. These changes they believe to have been in no way dependent on the formation of leaf gaps. They very rightly draw attention to the fact that herbs are by no means always characterized by multifasciculate stems as implied by Jeffrey and demanded by his hypothesis concerning the origin of the herbaceous habit. In many herbs there is a cylindrical xylem interrupted only by minute gaps associated with the departure of vascular traces to the

appendages, whilst in others the structure is multifascicular as has already been mentioned. Comparison of woody and herbaceous plants, in which each of these two types of structure occurs, shows that the multifasciculate arrangement persists in old stems of plants in whose young extremities it is at first

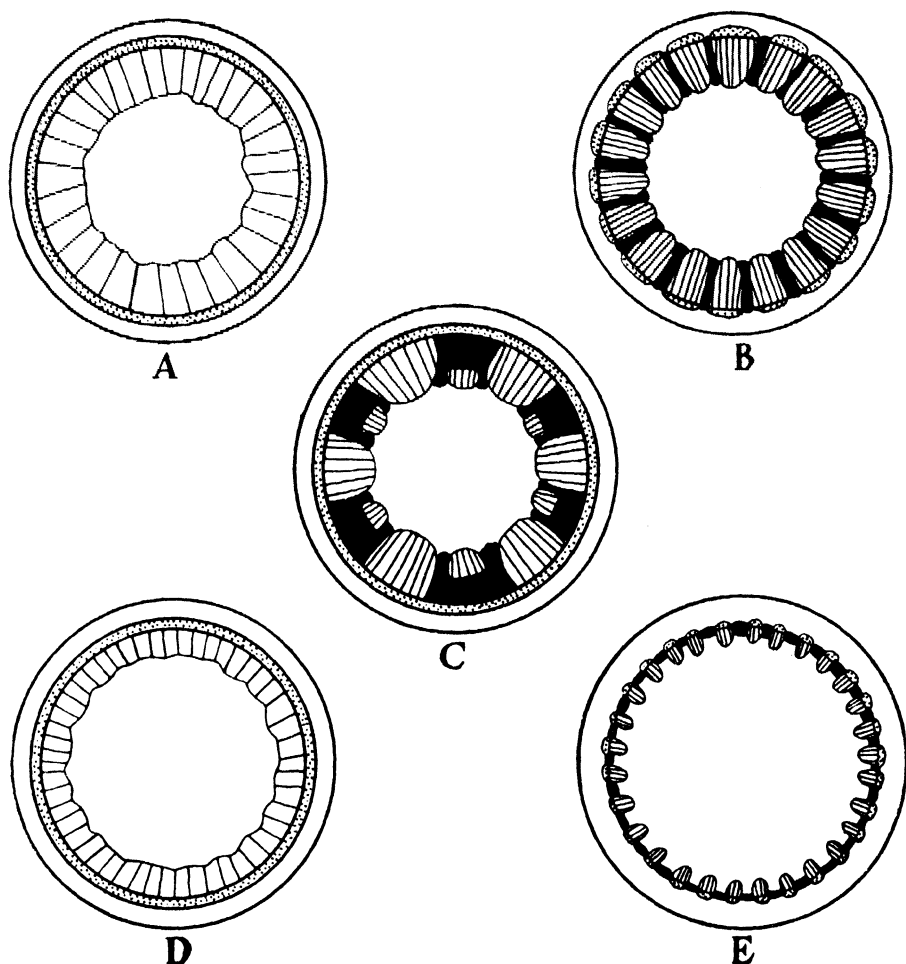


FIG. 3. A, Transverse section of one-year-old stem of arborescent or fruticose Dicotyledon, which is devoid of wide, high multiseriate rays. B, Transverse section of one-year-old stem of arborescent or fruticose Dicotyledon whose woody cylinder is dissected into separate strands by wide, high multiseriate rays. C, Transverse section of stem of woody or 'transitional' herb showing 'confronting' and 'flanking' parenchyma. This condition is emphasized by Jeffrey and Torrey in their theory of the origin of the herbaceous type. D, Transverse section of slender, herbaceous stem which is devoid of 'foliar storage rays'. E, Transverse section of slender, herbaceous stem whose stele is dissected into a series of discrete woody strands. (After Sinnott and Bailey 2113.) For further details see p. xxxvii.

established, whilst it is equally true that the closed cylinder of xylem persists in the older parts of the axis of those plants in which it is laid down when young. It has already been pointed out that Jeffrey and his co-workers based many of their conclusions on investigations of woody and herbaceous members of the Compositae which are multifasciculate when both young and old. Had

they extended their researches to a wider range of herbs it is probable that, like Bailey and Sinnott, they would have appreciated the difficulty of accepting the hypothesis that the progressive conversion of vascular tissue to parenchyma in the region of leaf insertions provided the sole explanation of the method by which herbs may have been evolved from trees. In 1914 Bailey and Sinnott also took exception to the foliar ray hypothesis on the following grounds. Firstly, if the hypothesis is correct, it is a necessary corollary that certain of the Amentiferae must be amongst the most primitive living angiosperms, and this they believed to be doubtful. Secondly, because multiseriate rays are known to have occurred in certain Dicotyledons from the middle and upper Cretaceous, i.e. at a period before the cooler climate of the Tertiary period began. It is difficult to understand why aggregation and subsequent compounding of rays should have occurred by then, especially as upholders of the theory stressed the importance of a cooler climate in inducing these alleged changes. Moreover the occurrence of plants with broad rays in tropical regions at the present time does not seem to indicate that low temperatures have been necessary for their formation. Thirdly, the evidence from seedling structure advanced in favour of the hypothesis is not always reliable, since the seedlings of certain oaks are known to include broad rays, and it is not true that the seedlings of *Quercus* differ *universally* from the adult in lacking broad rays. Fourthly, the interfascicular parenchyma of a multifasciculate axis is not always subtended by a tiny leaf-trace bundle as demanded by the hypothesis, but abuts directly on the pith tissue between strands of primary wood. By 1914 Bailey and Sinnott regarded the broad ray as having been evolved from a narrow type by simple enlargement which took place quite independently of the insertion of leaf-traces. To the present author it also seems that, if the foliar ray hypothesis were generally applicable, one would expect to find a very much dissected stele in plants in which leaves are particularly congested on the axis, and, conversely, a less dissected vascular system in plants with more widely spaced leaves. This is not in accordance with the facts, however, for if we examine a species of *Ranunculus* with widely spaced leaves we find a multifasciculate cauline vascular system. In woody members of the Ranunculaceae such as *Clematis* this is also true. In the woody species *Veronica traversii* or indeed in any of the woody members of this genus, in spite of the close approximation of the leaves on the axis, the xylem cylinder is interrupted only by small gaps which do not extend upwards and downwards in the axis to any appreciable extent, so that in transverse sections through an internode the closed cylindrical form of the xylem is maintained. The same applies in herbaceous species of *Veronica*. We thus have a striking example, and it is only one of the many that must occur, which strongly indicates that the degree of dissection of the cauline vascular system is not directly governed by the leaf-trace strands.

The essential difference between the attitude of Bailey and Sinnott on the one hand and of Jeffrey and Torrey and those with similar views on the other may perhaps be made clearer by the above series of diagrams (Fig. 3 A-E), after those in one of Sinnott and Bailey's (2113) papers. In A we have the primitive, arboreal angiosperm where wide rays flanking the leaf-traces are absent. In c the traditional structure of a herb is shown in which the foliar vascular strands are subtended on the outside and partly flanked by the

parenchyma of the foliar ray which is shown in black. By elimination of the subtending and retention of the flanking portions of the foliar ray tissue the polyfascicular type of stem (E) which is characteristic of advanced herbs is obtained. In the view of Bailey and Sinnott, the type of structure shown in E may, in some instances, have been derived from A through C as pointed out by Jeffrey and Torrey, but unlike the last two authors they also believe that the structure in E may have been derived directly from an arboreal ancestor with a structure like that shown in B merely by a reduction in cambial activity. In B there are well-marked flanking rays by which the xylem is broken up into separate bundles. In D is shown the structure of a herb in which the xylem forms a continuous cylinder, and this Bailey and Sinnott regard as having been derived from A, again by less prolonged cambial activity. To the present author the reasoning of Bailey and Sinnott appears simpler and more generally applicable than does that of Jeffrey and Torrey, although the two conceptions do not appear to be mutually exclusive in all cases. Whilst Bailey and Sinnott have clearly demonstrated the probable anatomical relationship between woody and herbaceous species which are closely related, their belief that arboreal forms were the sole ancestors of the modern angiosperms needs additional proof.

Thoday (2250), after making an intensive study of the stem of the sunflower (*Helianthus annuus*), concluded that there is no evidence of the derivation of herbs from trees by the conversion to parenchyma of segments of an originally continuous stele. His views are highly critical of the respective positions taken up both by Jeffrey on the one hand and Bailey and Sinnott on the other. Thoday does not believe that the ontogenetic development of the sunflower stem recapitulates its phylogenetic development. At the same time he does not appear to take exception to Bailey and Sinnott's idea that a herbaceous stem in all its essentials is like the first annual ring of its woody relatives.

Smith (2147), who has studied the nodal anatomy of *Acer*, *Platanus*, and *Quercus*, concurs with the view of Kostychev (1271, 1272) that a continuous procambium ring is the most common arrangement in the Dicotyledons, the dissected stele having been evolved by the conversion of segments to parenchyma. Smith believes, however, that far more ontogenetic work is needed before the phylogeny of the angiosperm stele can be profitably considered. It would be as well, before leaving the subject of rays, to recall that Stone (2204) expressed the opinion that these structures are to be regarded as 'stop-gap-tissue' of the same nature as callus, and that they occupy slits formed in the cambium cylinder caused by the increase in the periphery of the stem.

At this point it may be appropriate to consider the views expressed by Arber (30) who, unlike Bailey and Sinnott and many other botanists, believes the herbaceous habit to be primitive and the tree habit derived. She agrees that the floral characters of trees are often more primitive than those of related herbs, e.g. in the Leguminosae, Violaceae, &c., but points out that this may be due to the evolutionary lag in trees caused by the very fact that they are unable to pass through so many generations in a given space of time as is possible with herbs. The herbs therefore possess an evolutionary advantage, which enables genetical changes and consequently the formation of new species to proceed more quickly. Quoting Church's (424) *Thalassiphyta* she draws attention to the suggestion that when plants first emerged from a

marine to a terrestrial environment they were subjected to more intense insolation, resulting in an increase in photosynthesis and the incorporation of excess carbohydrate in the plant body. One result was a tendency for herbs to become transformed into trees, a tendency which may be kept in bounds in the youthful phases of a race, but one which may assume pathological proportions when the race becomes senile. She therefore regards the inert matter of a tree as in some respects comparable with the unbalanced development of useless growths which are known to have occurred in animals which are now extinct.

While, to the present writer, it seems somewhat distressing to have to regard the graceful giants of the forest as in any way pathological, it is as well to bear in mind, when discussing the phylogeny of herbs and trees, that much depends on precisely what is meant by the term 'origin'. Assuming that life began in the sea and migrated to land, it is difficult to imagine that this transmigration was effected by plants in any way comparable with modern arboreal forms. Plants of the migratory period were probably more like the modern herbs, so that on these purely speculative grounds the original land vegetation seems likely to have been herbaceous and the arboreal habit derived. In the modern era trees constitute the dominant element of tropical vegetation, and the geological record points to woody plants other than angiosperms as having made up a large proportion of warm climate vegetation of past ages. It therefore seems reasonable to imagine a primitively herbaceous vegetation having given rise to a mixture of herbs and trees quite early in the history of terrestrial vegetation. At this time climatic factors may have determined which of these two types of habit was dominant in a given region, just as they seem to have done in the present era.

It is true that a large proportion of fossilized plants which are known from the Devonian period until after the angiosperms first appeared in the early Cretaceous were arboreal, but there is no reason to suppose that herbaceous forms may not have existed simultaneously. May it not be true that in geological time herbaceous angiosperms existed in periods much preceding those from which we have any definite fossilized remains?

To the present author it seems quite possible that much of the difference of opinion concerning the origin of herbs and trees would disappear if it could be recognized that the terms 'herb' and 'tree' are commonly used in a very loose sense. Herbs of the *Linum*, *Veronica*, and *Galium* types, in which a continuous ring of xylem is differentiated almost at the growing apex of the stem, may be species which have evolved from arboreal ancestors by reduction of cambial activity. A herb of the *Ranunculus* type, with a cauline vascular system of widely spaced bundles, may, on the other hand, have been evolved from herbaceous ancestors which never included any arboreal or woody forms. We can thus see that 'herbs' may be of more than one type. By examining the structure of stems with this possibility in view, there seems a reasonable prospect that further information of considerable phylogenetic interest might be obtained.

Structure of the Node

Sinnott, and Sinnott and Bailey (2111, 2114) have put forward views concerning the phylogeny of the angiosperms which are based on a consideration

of the number of interruptions in the cauline vascular system which occur at a node, in connexion with the insertion of a single leaf. An extensive survey of fossil and modern plants showed that in some species the number of interruptions is three, in others only one, whilst in a third group the number is greater than three. Each separate interruption is caused by the attachment of an individual leaf-trace. The survey originally made by Sinnott led him to believe the trilacunar node to be primitive, whilst the unilacunar type as well as the nodes with more than three lacunae were regarded as more advanced. The phylogenetic development of the unilacunar from the trilacunar type is believed to have been caused in some cases by the elimination of two of the gaps and in others by closing together of three which were originally separate. The type of node was shown to be independent of the external morphology of the leaf. For example the number of gaps is not constant for all leaves possessing a sheathing base. Sinnott also found the number of gaps to be characteristic for a single family or even for a whole order, as in the Centrospermae, which were found to be unilacunar in all the material he examined. In other families such as the Ranunculaceae there was found to be far more variation.

Looking through the table in Sinnott's first paper in which he gives the distribution of each of the nodal types in some detail, it is striking to note the very clear demonstration that the trilacunar node occurs in many wholly unrelated families. It requires rather a stretch of the imagination to regard all of these families as primitive, and even Sinnott himself admits in his paper that there are numerous exceptional plants that do not fit in with his main thesis. It would also be interesting to have more information concerning the constancy of the type of node in different species of a large genus.

Sinnott and Bailey (2112) seem rather less certain than Sinnott was in his earlier paper in the same year that the type of node is independent of the external form of the leaf. In their joint paper the authors point out that a majority of plants with trilacunar nodes possess stipules, whereas, with certain exceptions, stipules are absent from those with unilacunar nodes. The same authors emphasize that leaves with a multilacunar node possess a sheathing base, and also express the view that the growth of the lateral leaf-traces stimulates the development of stipules since the stipule was invariably found to occur directly opposite the point of departure of the trace. At the same time they point out that stipules are generally absent from families in which the leaf margin is entire even when the node is trilacunar. Bailey and Sinnott were somewhat uncertain about the morphology of stipules but inclined to the idea that they are homologous with leaf teeth. In fact stipules, sheaths, ligules, and similar structures at the base of the petiole are, in their opinion, all homologous 'since they are dependent in position and character on the anatomy of the node'.

Sinnott and Bailey (2114) further expressed the opinion that the palmate is phylogenetically more primitive than the pinnate type of leaf, and again based their conclusions on evidence derived from nodal anatomy, palaeobotany, and comparative morphology. →

PHYLOGENETIC EVIDENCE FROM WOOD ANATOMY

The controversy about the foliar ray hypothesis and its bearing on the possible derivation of herbs from trees has been described above (p. xxxiv).

Another subject that was highly controversial during the same period concerned the origin of the vessel in the Gnetales. It was thought that this group, owing to its possession of vessels and the occurrence of broad, angiosperm-like rays in some species, might prove to be a link between other gymnosperms and the angiosperms. The controversy centred round the problem of whether the simple perforations in the end-walls of the vessel members ('elements') of the Gnetales and angiosperms respectively have been developed phylogenetically along the same lines. From the outset it appeared unlikely that the vessel had had precisely the same origin in both groups, because the less advanced perforation plates in the Gnetales are typically 'Ephedroid' or 'foraminate', that is pierced by irregularly arranged, circular holes, whereas the corresponding primitive multiperforate plates of the Dicotyledons are scalariform, with regularly arranged, elongated holes.

It is generally believed that the ancestral tracheal element was the tracheid, a long cell with bordered pitting, and that vessels have been derived from tracheids by the disappearance of the pit-membrane from some of the pitting in the overlapping walls, thus forming a vertical series of cells that gives an uninterrupted passage for water. Thompson (2255) in 1918 postulated that the simple perforation of the Gnetales must have been derived from tracheids with circular bordered pits, whereas those of the angiosperms must have been derived from tracheids with scalariform pitting, and that therefore there can be no genetic connexion between the vessels of these two groups. He considered, rather, that the vessels of the two groups furnish a remarkable instance of the independent development of similar structures.

This view was strongly opposed at the time, particularly by Bliss (207), Jeffrey, and MacDuffie (1408), but has been supported by the more recent studies of the development of the vessel that are discussed later, and is now generally accepted. The principal arguments against Thompson's views were the occurrence of a few scalariform perforation plates in *Gnetum* and of occasional foraminate plates, similar to those of *Ephedra*, in some genera of the Rosaceae and in *Paonia* and *Tropaeolum*. Bliss also held that scalariform pitting had its origin in the fusion of multiseriate circular pits. This latter view has not been upheld by subsequent research and it seems highly probable that the occasional foraminate perforation plates of the Rosaceae represent a sporadic development from existing circular intervascular pitting in the side walls, in much the same way as occasional reticulate perforation plates in the highly specialized vessels of the Bignoniaceae appear to be related to the hexagonal, alternate intervascular pitting.

Bailey (75) has recently returned to this problem as the result of ontogenetic studies of the primary and secondary xylem. He considers that vessels arose first in the secondary xylem and later in the last-formed part of the primary xylem, i.e. where the secondary walls of the tracheary elements are pitted, and that specialization in the primary xylem thus lags behind that of the secondary xylem. He points out that Dicotyledons whose vessels in the secondary wood are very unspecialized often possess vessels in the primary xylem that are barely distinguishable from scalariformly pitted tracheids. He states that 'the fact that structurally primitive angiosperms had scalariformly pitted tracheids, from which vessels originated, rules out any possibility of deriving the angiosperms from the Gnetales or other representatives of the

higher gymnosperms. 'The Ginkgoales, Coniferales and Gnetales are characterized by having a highly specialized and peculiar type of primary xylem which is entirely unlike that of other known vascular plants, with the possible exception of the Ophioglossales.' 'The development of the vessels in the Gnetales from circular pitted tracheids he concludes to be unique and 'entirely unlike the derivation of vessel members from scalariformly bordered-pitted tracheids in *Selaginella*, *Pteridium*, monocotyledons and dicotyledons'. Bailey, indeed, considers that vessels have originated independently not only in the Gnetales and angiosperms, but in five distinct categories of the Tracheophyta, namely the Selaginetales, Filicales, Gnetales, Monocotyledons, and Dicotyledons.

In 1918 Bailey and Tupper published a paper (100) on size variation in tracheary cells, which marked the beginning of a new period of phylogenetic wood anatomy. The significance of this work does not seem to have been immediately appreciated, and it was not till Frost (728-30) applied this work to the development of the vessel member that it was realized that there was to hand a new tool of the greatest importance. The main conclusion reached by Bailey and Tupper can be stated very simply—that the length of the tracheary elements and of the cambial initial is reduced as specialization increases. The special value of this investigation lies in the fact that it was based on observations over such a wide range of plants—from the Cycadales to the angiosperms, and including various fossil plants—that, as Tippe (2261) has said, it can be fairly claimed that the conception of reduction in length as an index of specialization is not based on any system of angiosperm classification and is independent of any preconceived notion that this or that group of the gymnosperms has given rise to the angiosperms; or any idea that the Ranales or the Amentiferae are primitive. Consequently it offers a means of breaking the vicious circle caused by a taxonomic group being regarded as primitive or advanced because its floral characters are primitive or advanced, the floral characters themselves being judged as primitive or advanced because they occur in primitive or advanced groups.

Frost correlated vessel member length with various other characters, of which the most important was the nature of the end-wall. He concluded that the scalariform perforation plate with many bars set in a very oblique end-wall is the most primitive type because it is associated with the longest vessel members; he also concluded that subsequent specialization has taken the form of a progressive reduction in the number of bars and perforations and in the steepness of the end-wall to a single, simple perforation in an almost horizontal end-wall. The relation between this series and vessel member length is shown in the following table, taken from Frost.

TABLE I
Vessel Member Length and Type of Perforation Plate

<i>Perforation plate</i>	<i>Number of species</i>	<i>Member length mm.</i>
Entirely scalariform . .	52	1.09
Scalariform and simple . .	19	0.81
Oblique and simple . .	34	0.69
Transverse, simple . .	169	0.40

Frost applied a similar technique to intervacular pitting and demonstrated a series with scalariform pitting as the most primitive, progressing through transitional types to opposite and finally to alternate. The relation between these types and vessel member length, as demonstrated by Frost, is shown in Table 2.

TABLE 2
Vessel Member Length and Intervascular Pitting

<i>Intervascular pitting</i>	<i>Number of species</i>	<i>Member length mm.</i>
Scalariform . . .	15	1.13
Transitional . . .	28	1.07
Opposite . . .	33	0.79
Alternate . . .	183	0.46

The validity of this work is now generally accepted and the same technique, applied to other characters in wood, has helped to demonstrate other phylogenetic series. The results make possible many interesting comparisons of the relative specialization of different groups of the angiosperms. Before discussing this later work in more detail, it is perhaps advisable to point out that individual measurements of vessel member length based on single samples must not be interpreted too exactly, as cell dimensions vary considerably under different conditions and in different parts of the stem (see p. xxiii). Further, most of this work is based on the assumption, probably quite legitimate when based on large numbers of observations, that characters constantly or predominantly associated with long tracheary elements are themselves primitive.

Using the series of vessel characters established by Frost (729) as phylogenetic indicators and a similar statistical technique, Kribs (1286) has defined certain types of ray, which are believed to exhibit degrees of specialization. His conclusions may be summarized as follows. The most primitive ray type consists of a combination of multiseriate rays with high uniseriate 'wings', and numerous and high uniseriate rays composed of high upright cells. (Plate C, Heterogeneous I). Specialization takes the form of reduction either of the uniseriate rays, leading to a type with multiseriate rays only (Plate C, Homogeneous II), or of the multiseriate rays, leading to types with wholly uniseriate rays (Plate C, Heterogeneous III and Homogeneous III). Parallel with reduction of the uniseriate or of the multiseriate rays, individual rays become less heterogeneous and the component cells smaller. Wholly uniseriate rays are never primitive, being derived from multiseriate types, those derived from less advanced types tending to be heterogeneous with large cells.

Kribs's views on the most primitive type appear to be generally acceptable, but his assumption that reduction of either the multiseriate or the uniseriate rays is always accompanied by a decrease in heterogeneity cannot be completely justified and leads to an over-simplification of the problem. It has been objected by Barghoorn (138) that reduced cambial activity, such as occurs in shrubs, is often accompanied by the retention or exaggeration of heterogeneity. Such plants may retain a primitive type of ray, e.g. high-celled uniseriate rays, or there may be a tendency to axial elongation of the ray cells, converting procumbent cells to upright cells. These woods may

thus be specialized in so far as their rays are wholly multiseriate or wholly uniseriate, yet the rays may be composed entirely of high upright cells. There is no place in Kribs's classification for such rays. The tendency to axial elongation of the cells may in extreme cases convert all the ray initials to fusiform initials and result in a wood with no rays, e.g. in *Bocconia*, *Santolina*, and *Sesamum*.

Type of perforation plate is a much more convenient index of specialization than vessel member length, as the latter can be satisfactorily measured only in slides of macerated material; the relation between the two characters appears to be sufficiently close to justify the use of type of perforation alone. One shortcoming of this method, however, is that more than half the species lie in the most advanced group obtainable with this feature—perforations simple and end-walls transverse. This large group, however, can be subdivided by the use of storied structure to distinguish the most highly specialized woods.

It has been shown by Beijer (168) and others that storied structure (see p. xxvii) is related to the length of the cambial initial. The number of cells in the cambium is constantly being increased to keep pace with its increasing perimeter as the stem grows in girth. In most woods this increase in the number of cambial cells is obtained rather indirectly, through the occasional division of an initial into two halves by the formation of a horizontal cross-wall; the two halves subsequently elongate till they overlap for a large part of their length and so constitute two cells approximately side by side. This is typical of woods with long cambial initials. In woods in which the mean length of the initials is less than about 0.4 mm. the plane of division changes and, instead of a small transverse wall, the cell forms a long radial wall. This gives rise to two cells almost exactly side by side and, when repeated, to a horizontal series of initials lying side by side, and so to storied structure in the wood. Storied structure, therefore, being associated with very short cambial initials, can be used as an index of a very high level of specialization.

Data from about 1,800 woods¹ have been classified by the author into the following groups of increasing specialization:

- I. Perforation plates wholly scalariform (206 woods).
- II. Perforation plates scalariform and simple (91 woods).
- III. Perforations all simple, elements not storied (1,261 woods).
- IV. Perforations all simple, rays or parenchyma storied (243 woods).

The percentages of the woods of each group exhibiting particular features are given in Tables 3–5. In these tables each figure represents the percentage of all the woods in one Group with a particular feature. For example, 132 out of the 206 woods in Group I, or 65 per cent., have scalariform to opposite pitting; the 35 per cent. of this Group that have other types of pitting are not referred to in this table.

¹ Many of the data accumulated during the writing of this book were recorded on 'punched cards', and correlations between different features could then be simply obtained by counting the numbers of cards punched for particular features. In general one card was used for each species, but where a species was sufficiently variable it was necessary to use more than one card for it, or, conversely, where species could not be distinguished, more than one species may be represented by a single card. Such exceptions, however, are not sufficiently numerous to mask any clearly marked trend and in any case tend to cancel each other out. More species were grouped than were given more than one card per species.

TABLE 3

Features associated with a Low Level of Specialization

Feature	Groups in order of increasing specialization				Average %
	I <i>Perforations scalariform only</i> (206 woods) %	II <i>Perforations simple and scalariform</i> (91 woods) %	III <i>Perforations simple, not storied</i> (1,261 woods) %	IV <i>Perforations simple, storied</i> (243 woods) %	
Intervascular pitting scalariform to opposite	65	33	2.5	0.4	11
Vessels exclusively solitary	35	10	15	5	16
Fibres with distinctly bordered pits	73	45	31	7	33
Parenchyma diffuse	65	45	33	23	36

The proportion of woods with scalariform and opposite intervacular pitting shows the progressive decrease from Group I to Group IV that would be expected from Kribs's work and calls for no special comment. The next feature, exclusively solitary vessels, has been claimed, e.g. by Tippo (2261), to represent an unspecialized type. This is confirmed by the above figures, the percentage dropping from 35 in Group I to 5 in Group IV. The figures in this table also confirm that both fibres with distinctly bordered pits and diffuse parenchyma are unspecialized. Specialization in the fibres appears to have proceeded from the fibre-tracheid, with large bordered pits in all walls touching other fibre-tracheids and numerous pits to vessels, towards the libriform wood fibre, with small, simple to slightly bordered pits on the radial walls between fibres and with few or no pits to vessels. Specialization appears also to have been accompanied by a greater proportional elongation of the developing fibre, so that, while fibre-tracheids are seldom more than one and a half times as long as the cambial initial from which they were derived, libriform fibres are commonly two or three times and may be up to eight or nine times (374) as long.

The figures for diffuse parenchyma differ in some respects from those given by Kribs in his study of the specialization of parenchyma (1287), particularly the persistence of diffuse parenchyma in the highest group (23 per cent. in Group IV). In Kribs's highest group, woods with transverse simple perforations, the percentages are 0 for 'diffuse' and 2.7 for 'diffuse-aggregate'. This discrepancy may perhaps be accounted for if Kribs included only genera in which these types are dominant, as the author's figures include all species in which diffuse parenchyma occurs, irrespective of other types in the same wood. It seems probable that there is a more advanced type of diffuse parenchyma, possibly Kribs's 'diffuse aggregate', which should, if possible, be distinguished from the unspecialized type.

The figures given in the table below fully bear out the view that homogeneity in rays is an advanced character. It is also apparent that paratracheal parenchyma in some form or other is more commonly associated with advanced than with primitive woods, the percentage of woods with predominantly paratracheal parenchyma rising steadily from 14 in Group I to 57 in Group IV. Of these paratracheal forms aliform and confluent appear to be the most

TABLE 4
Features associated with a High Level of Specialization

Feature	Groups in order of increasing specialization				Average %
	I Perforations scalariform only %	II Perforations simple and scalariform %	III Perforations simple, not storied %	IV Perforations simple, storied %	
Rays homogeneous	24	9	21	37	21
Parenchyma predominantly paratracheal	14	34	47	57	44
Parenchyma aliform or con- fluent	3	9	22	60	24

advanced. This is in general agreement with the conclusions of Kribs (1287), who, using a similar technique based entirely on type of perforation and slope of end-wall, placed his parenchyma types in the following sequence and correlated them with vessel member lengths (given in brackets): diffuse (0.92 mm.), absent (0.78 mm.), diffuse aggregate (0.65 mm.), vasicentric scanty (0.60 mm.), metatracheal narrow (0.51 mm.), terminal (0.44 mm.), metatracheal wide (0.42 mm.), vasicentric abundant (0.31 mm.). Other conclusions drawn by Kribs were that the absence of wood parenchyma indicates a primitive condition, that terminal parenchyma is a specialization due to reduction and that, as wood becomes more highly specialized, the individual wood parenchyma cells become shorter and wider.

The number of cells in a single strand of parenchyma can also be used as an index of level of specialization. Long cambial initials that give rise to strands of 8 or more cells are characteristic of unspecialized woods. Strands of 1-2 cells and numerous fusiform parenchyma cells are most frequent in highly specialized woods. The tendency for the number of cells to decrease as the strands become shorter in length is, however, partially offset by the parallel tendency, mentioned above, of the cells to become shorter as they become more highly specialized.

TABLE 5
Miscellaneous Features

Feature	Groups in order of increasing specialization				Average %
	I Perforations scalariform only %	II Perforations simple and scalariform %	III Perforations simple, not storied %	IV Perforations simple, storied %	
Minute, alternate, inter- vascular pitting	6	12	22	19	19
Septate fibres	21	36	22	7	21
Ring-porous (in 3000 woods)	3	3	4	4	4
Vessels spirally thickened (..)	15	16	9	8	8

Minute, alternate, intervascular pitting might logically be assumed to represent the end of the series scalariform—opposite—alternate and so be a very advanced character. From Table 5 it will be seen that though it is less common in Groups I and II, as would be expected from the mere fact that it

is a form of alternate pitting, there is no significant difference between the proportion of woods with this feature in Groups III and IV. It is suggested that minute pitting represents a special development peculiar to particular groups rather than a form of specialization towards which the vessels of all moderately advanced woods tend. This feature is likely, therefore, to prove of value as an index of affinity rather than of level of specialization.

Septate fibres tend to be of common occurrence throughout large natural groups, such as that which includes the Meliaceae and Burseraceae, and are a most useful index of affinity. Opinion is divided as to whether they represent an advanced or a primitive type of fibre. Chalk (354) in 1937 suggested that they should be regarded as more primitive than the non-septate libriform fibre, but Tippo (2261) a year later reached the opposite conclusion from his study of the woods of the Moraceae and their presumed allies. The figures given in Table 5 show that septate fibres occur just as commonly in primitive as in moderately advanced woods (Groups I-III), but that they are far less frequent in the most advanced woods (Group IV). A list of the families in which septate fibres occur is given on p. 1351.

Ring-porousness, or the development of a marked zone of larger vessels at the beginning of the growth ring, appears to be accompanied by an increase in the length of the complete vessels in the pore zone, and has been shown by Huber (1102) to increase the rate of flow of water through the wood. It is associated with cold winters or alternating very dry and wet seasons and has been generally assumed to be a specialized development of either an ecological or an evolutionary nature, though the actual evidence adduced has been rather slender. Recently Gilbert (765) has investigated this problem afresh, using both the older approach of Jeffrey, based on recapitulation and supposedly conservative parts of plants, and the newer technique introduced by Frost. Gilbert has concluded that 'there is abundant evidence to indicate that the ring-porous type of vessel arrangement represents an evolutionary advance from the diffuse distribution'. He states that in any genus the ring-porous species have other advanced characters, compared with the diffuse-porous species, and that, within the north temperate regions, ring-porousness is correlated with other specialized characters, such as simple perforations, paratracheal parenchyma, and simple pits in the fibres, but that it is not correlated with ray types as defined by Kribs (1286). He considers that this specialization took place early in angiosperm history and affords no proof of parallel lines of development.

Gilbert emphasizes strongly that morphological comparisons are valid only with species from the limited region of the world in which ring-porousness seems to have developed, and that the feature is absent from the temperate regions of the southern hemisphere. This may account for the fact that the regression shown in Table 5 between ring-porousness and degree of specialization is not significant statistically, as judged by the χ^2 test,¹ as the data were

¹ The relevance of this test is somewhat doubtful owing to the tendency of related woods to give similar records of occurrence or non-occurrence of a particular character. This applies to all the features measured, but those given in Tables 3 and 4 have such exceedingly large χ^2 values that the significance can scarcely be in question. For the features, other than ring-porousness, in Table 5, the differences are not significant according to the χ^2 test, but the comparatively steady trend of the percentages suggests that there is a real trend from Group I to Group IV, though this cannot be so firmly established as for the other features.

drawn from all over the world. It is to be noted, however, that the population on which Gilbert bases his conclusions has some peculiar features, and neither his ring-porous nor his diffuse-porous group corresponds with material from the wider geographical range investigated by the author. For example, 85 per cent. of the species in his ring-porous group have paratracheal parenchyma and 27 per cent. in his diffuse-porous group, compared with 50 and 42 per cent. for the author's material. The proportion of woods with scalariform perforation plates in Gilbert's whole group of about 60 species is rather higher (22.5 per cent.) than for the author's 1,800 woods, but, whereas Gilbert's woods did not include a single ring-porous species that had scalariform perforation plates, the author's data included several.

The relation between the features discussed by Gilbert and the occurrence of ring-porousness in the material examined by the author is shown in the following table.

TABLE 6
Comparison of 128 Ring-porous with 2904 Diffuse-porous Woods

<i>Feature</i>	<i>Percentage of ring-porous woods</i>	<i>Percentage of diffuse-porous woods</i>
With diffuse parenchyma	32	35
With predominantly paratracheal parenchyma	53	47
With fibres with distinctly bordered pits	32	30
With homogeneous rays	22	18

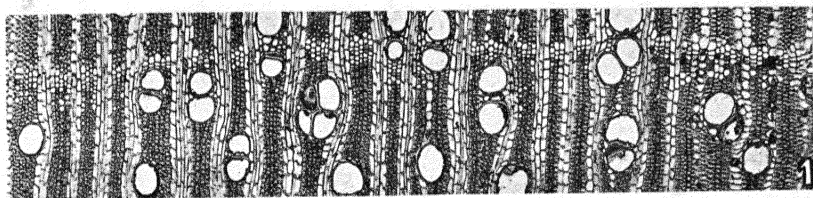
For each feature the difference between the numbers of woods with and without the feature in the ring-porous and the diffuse-porous groups was subjected to the χ^2 test, and in no case was the difference found to be significant.

It would appear unwise, therefore, to rule out the possibility that ring-porousness may represent an ecological specialization, which occurs in wood at very different levels of general specialization and in widely separated taxonomic groups (for list of families see p. 1350).

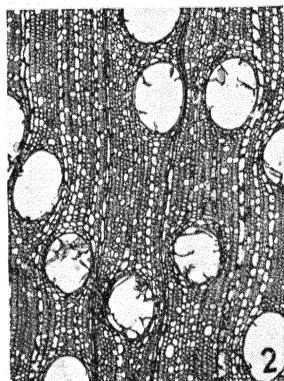
Spiral thickening of the secondary wall of the vessel is regarded by Frost (730) as an advanced character. In the material examined by the author, however, spiral thickening was relatively more common in unspecialized than in specialized woods; it will be seen that in Table 5 the percentage of woods in which spiral thickening occurs drops from 15 per cent. of Group I to 8 per cent. of Group IV. Spiral thickening is much more closely linked with ring-porousness. Of the diffuse-porous woods tabulated only 140 out of 2,780 woods (6.5 per cent.) possessed spiral thickening, while among the ring-porous and semi ring-porous woods 125 out of 289 (44 per cent.) had this feature. It is possible that it is the ecological factors associated with ring-porousness that are primarily responsible for this correlation. Spiral thickening occurs sporadically in many widely separated families (for list see p. 1349).

So far, wood anatomy has been discussed mainly as an index of general specialization, and it remains to consider how it may be used to demonstrate affinity. The fact, so important for the former purpose, that the number of characters in wood is small and that each of the elements has tended to follow one general trend of specialization, to some extent limits the use of wood anatomy for this purpose. Paucity of characters also implies the probability

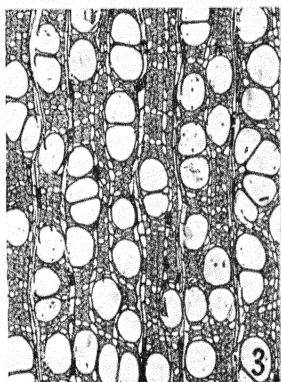
PLATE A APOTRACHEAL PARENCHYMA



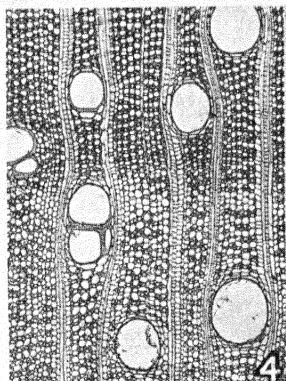
TERMINAL



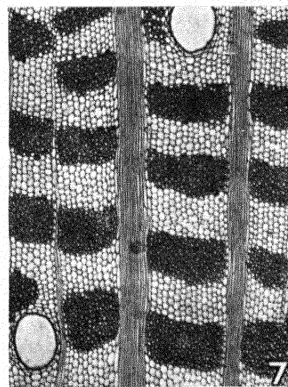
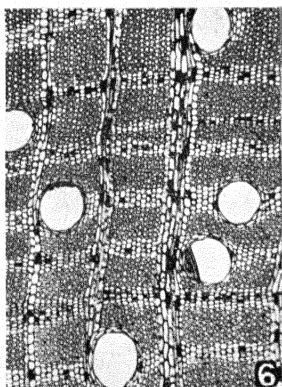
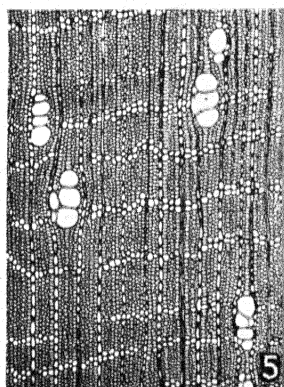
Scattered



Diffuse-in-aggregates

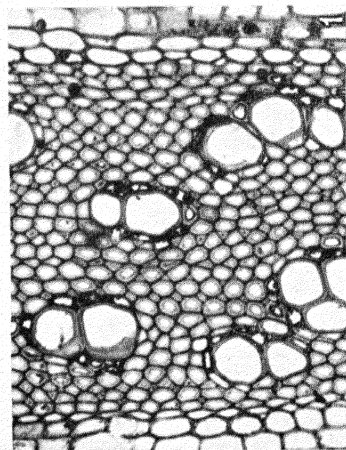


DIFFUSE

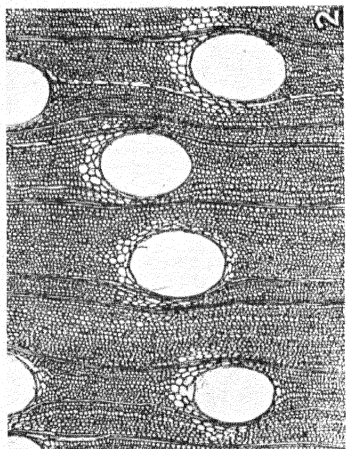


METATRACHEAL OR BANDED

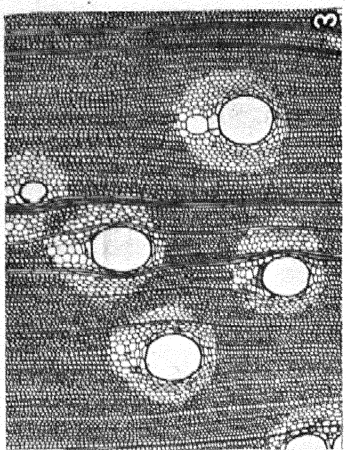
PLATE B PARATRACHEAL PARENCHYMA



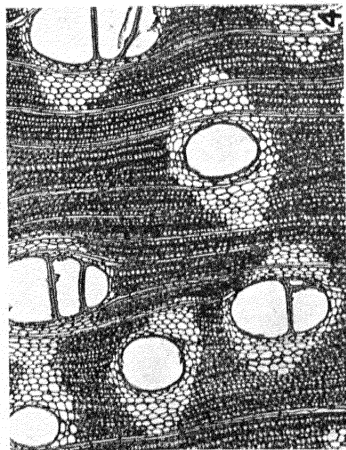
SCANTY



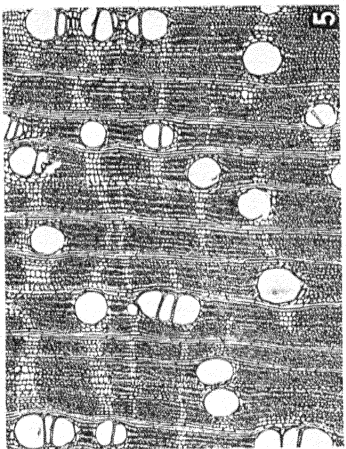
ABAXIAL



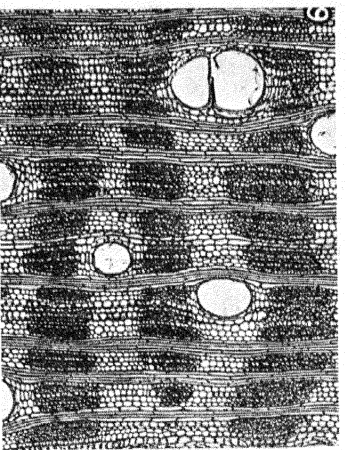
VASICENTRIC



ALIFORM

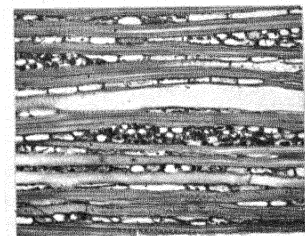


ALIFORM-CONFLUENT

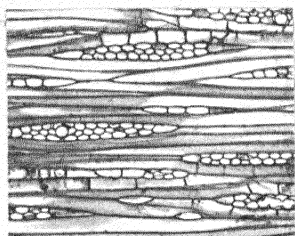


CONFLUENT

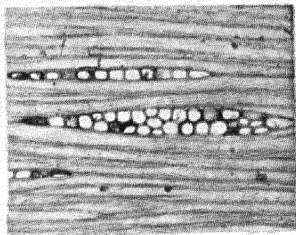
PLATE C RAY TYPES (based on Kribs 1286)



I

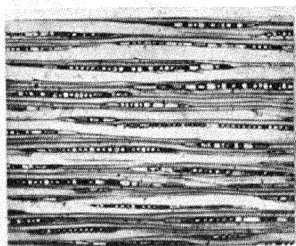


II A

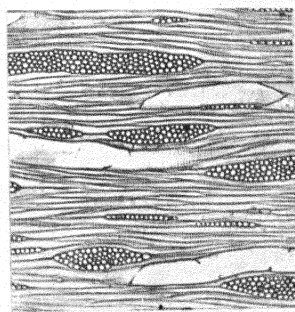


II B

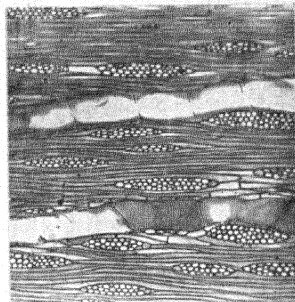
HETEROGENEOUS



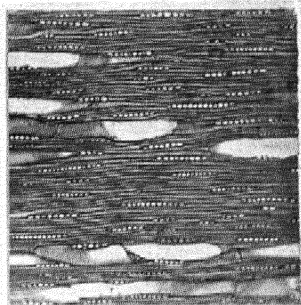
III



I



II
HOMOGENEOUS



III

of many cases of parallel development. If two or more taxonomic groups have but one important character in common, this should be regarded as suggestive rather than as proof of affinity, unless supported by other evidence. There are some special lines of development limited to well-defined groups, such as tile cells in the Bombacaceae and Sterculiaceae. It is, however, not only unusual characters that are of special taxonomic interest, but also unusual combinations of common characters. This is, perhaps, particularly true of characters that indicate specialization, where one feature is at a markedly different level from the others. For example, *Betula* is characterized by vessels with exclusively scalariform perforation plates, but minute, alternate intervascular pitting, the former being an unspecialized feature and the latter an advanced one. Similarly, in the Zygophyllaceae there is an unusual combination of storied structure (specialized) with distinctly bordered pits in the fibres (unspecialized).

The significance of the more important characters of the wood, not already described on pp. xxi–xxvii, is discussed briefly below.

Vessels

The most valuable taxonomic vessel characters are the distribution and pattern of the pores as seen in transverse sections. The majority of woods have a preponderance of solitary vessels, mixed with some multiples of two or three cells. Divergence in either direction—to exclusively solitary vessels or to more numerous or larger groups and multiples—is useful for identification, but the possession of exclusively solitary vessels, being a common unspecialized type, cannot be used alone as indicating affinity. In some groups there is a marked tendency for multiples to be more common or for the vessels to be arranged in radial, oblique, or tangential lines, and these characters can be used positively as indicating affinity. They cannot, however, be safely used negatively as evidence of lack of affinity with woods without any such pattern. The marked radial or oblique pattern known as ‘dendritic’ (see Fig. 175 A), however, seems to lack any such significance, as it occurs sporadically in isolated genera in many widely separated families (for list see p. 1351). It has already been mentioned that minute, alternate, intervascular pitting tends to be characteristic of large natural groups; the same may possibly be true of very large alternate pitting. The nature of the pitting between vessels and ray or wood parenchyma cells also appears to have some taxonomic significance, particularly the distinction between pitting that is essentially similar in size and shape to the intervascular pitting, and that which includes some much larger, and often irregularly shaped pits, one or other of these types commonly persisting throughout a family or larger group. The feature known as a ‘vestured pit’ (formerly ‘cribriform membrane’) has been shown by Bailey (78) to be characteristic of a limited number of families (for list see p. 1350). Vasicentric tracheids tend to be associated with particular taxonomic groups, but are characteristic of tribes rather than families (for list of families see p. 1351).

Parenchyma

This is possibly the most important tissue indicating relationship, but, in the present state of knowledge, is also the most difficult to interpret. Probably the most fundamental distinction is that between apotracheal and paratracheal

parenchyma (see Plates A and B), and in most families the parenchyma is wholly or predominantly one or the other. In a few groups, e.g. in the Malvales and in some of the Dipterocarpaceae, both types may be common in the same wood, but this is sufficiently rare for it to constitute a distinctive character. Some of the banded types are difficult to interpret as definitely apotracheal or paratracheal. Parenchyma also tends to be rather variable in type, particularly under conditions that cause the amount to vary. This is true not only of different specimens, but even of different parts of the same ring, it being common, for example, for parenchyma to be more banded in the outer part of the ring. Such variation, however, seldom affects the fundamental difference between apotracheal and paratracheal and appears to represent merely a step up or down in a series, e.g. from aliform to confluent or from scattered diffuse cells to short apotracheal lines (diffuse-in-aggregates). Use may be made of this variation for the interpretation of banded types; where parenchyma is least abundant in a species, either in particular rings or parts of a ring or in different specimens, it will usually be found that, if the bands are essentially paratracheal, the parenchyma will be broken down to aliform-confluent types, whereas if the bands are apotracheal, there will be some vessels without any parenchyma round them. Very little appears to be known about the influence of external factors on such variation.

Single crystals of calcium oxalate scattered in the ordinary cells of wood- or ray-parenchyma are too common to be of much value, but chambered crystalliferous cells and special forms of crystal, such as raphides and druses, are of significance, as is the occurrence of silica and of less common inclusions such as lapachol (1789) and aluminium (2515).

Rays

Most ray characters, such as heterogeneity and the number of uniseriate rays, indicate general level of specialization rather than affinity. Size, particularly the maximum number of cells wide, is sometimes characteristic of taxonomic groups, e.g. the large rays of the Proteaceae and Rhizophoraceae and the small rays of the Salicaceae. On the other hand, there is no reason to suppose that ray size in itself indicates affinity between groups that are widely separated on other grounds. Further, it must be remembered that exclusively uniseriate rays are a form of specialization that has occurred independently in occasional genera of many families.

One of the standard features used in wood descriptions is 'rays of two sizes'. In some woods, e.g. in *Quercus*, the rays are either uniseriate or many cells wide, with no intermediate sizes. On the other hand, in *Fagus*, the rays of which are also often described as being of two sizes, all the intermediate widths between uniseriate and the maximum number of cells can be found. Without more adequate definition the feature has little significance. It seems probable that it is associated with the relatively uncommon method of increasing the ray tissue, to keep pace with increasing girth, by the splitting up of large primary rays and the subsequent growth of the parts split off to the maximum size.

Fibres

It has already been mentioned that septate fibres afford a valuable indication of affinity, and that they occur commonly throughout large and small

groups that are considered to be closely related on other grounds (for list of families see p. 1351).

Intercellular Canals

Normal canals are of very limited occurrence and tend to be characteristic of particular groups. For example, the Dipterocarpaceae typically have vertical canals and the Anacardiaceae and Burseraceae commonly have radial canals. A tendency to form canals in response to injury also tends to be characteristic of taxonomic groups, e.g. the Meliaceae (for list of families with intercellular canals see p. 1353).

Vestal (2329), using a technique similar to that of Frost, concluded that the phylogenetic value of anatomical studies rests mainly on the fact that the characters employed are quite different from the exomorphic ones that are normally employed by taxonomists. It is thus possible to obtain an entirely independent check on the conclusions of the orthodox taxonomist. Vestal (2330) also points out other strengths and weaknesses of the anatomical method of testing phylogeny, and rightly emphasizes that anatomical characters can be successfully used only to supplement exomorphic features.

Heimsch and Wetmore (939) have shown how, by using those characters of the secondary xylem which they describe as being generally accepted indicators of phylogenetic development, it is possible to show specialization tendencies within a family. It was found possible to arrange the constituent genera of the Juglandaceae in a phylogenetic sequence that agrees in nearly all details with one already prepared by Manning (1432), working with the exomorphic features.

Chalk (354) has drawn attention to the fact that parallelism between the wood structure and the accepted systems of classification tends to break down in groups larger than the family. He has compared the evidence for a particular phylogenetic sequence derived from wood structure with the arrangement in each of the taxonomic systems of Bentham and Hooker, Engler, and Hutchinson. Hutchinson's arrangement of the Archichlamydeae was found to agree more closely with the evidence from wood structure than does that of Engler. Other conclusions drawn were that:

'The Monochlamydeae of Bentham and Hooker appears to be slightly less highly specialized than the Polypetalae, but neither group differs very markedly from the average for all the Dicotyledons examined. The Metachlamydeae (Sympetalae) includes a mixture of specialized and unspecialized woods, but these can be separated by the type of parenchyma present. The woods of Engler's Primulales, Plumbaginales, Contortae (part), Tubiflorae and Campanulatae have paratracheal parenchyma and constitute a highly specialized group.'

CONCLUSIONS

The main emphasis in recent years has been on the anatomy of the secondary xylem and in particular on the evolutionary trends of its elements. At present direct comparison between woody and non-woody plants is not possible, but work on anatomical specialization in secondary wood suggests that the application of this knowledge and of similar techniques to the xylem and

other tissues of the non-woody plants may ultimately make such a comparison feasible. Tippo (2264) has said:—

‘There is every reason to suppose that the trends already defined will be found to prevail in the secondary wood of the herbs, and there is also some basis for the belief that similar sequences will be unearthed in the primary xylem. Bailey (75), for example, has recently shown that the evolutionary development of the vessel elements in the primary xylem parallels the development of these structures in the secondary xylem.’

The recent work of Cheadle (382-8) on the systematic anatomy of the Monocotyledons indicates other lines along which further advances are likely to be made.

There seems to be a considerable body of evidence in favour of regarding the Magnoliaceae and their allies as retaining many primitive characters. This is supported especially by the lack of vessels in their allies, the homoxylous angiosperms *Drimys*, *Trochodendron*, and *Tetracentron*. This, in all probability, is to be regarded as the retention of a truly primitive character rather than as a reduction. Modern views as to the origin and specialization of the vessel, particularly those concerned with the derivation of perforations from bordered pits, appear to rule out any possibility of deriving the angiosperms from the Gnetales (75).

It thus seems probable that one line of descent among the angiosperms started with forms, possibly now extinct, which were in some respects similar to the modern Winteraceae, Trochodendraceae, and their allies. This conclusion is in accord with the views of many taxonomists who work with floral and other exomorphic characters, and also with the views expressed by Wieland (2421).

The main general conclusions to be drawn from studies of the vessel have been summarized by Bailey (75) as follows:—

‘The independent origins and specializations of vessels in monocotyledons and dicotyledons clearly indicate that, if the angiosperms are monophyletic, the monocotyledons must have diverged from the dicotyledons before the acquisition of vessels by their common ancestors. This renders untenable all suggestions for deriving monocotyledons from vessel-bearing dicotyledons or *vice versa*. Furthermore, the highly specialized structure of the xylem throughout both stems and roots of herbaceous dicotyledons, not only affords conclusive supplementary evidence of the derivation of herbaceous from arboreal or fruticose dicotyledons, but also is an insuperable barrier to the derivation of monocotyledons from herbaceous dicotyledons.’

There seems to be some danger in assuming too readily that all modern angiosperms have been derived from Magnolian or allied ancestors. It is possible that a Magnolian stock may have provided the sole starting-point for the evolution of the angiosperms, but, if this be so, it is somewhat remarkable to find evidence of the co-existence of wholly unrelated flowering plants so long ago as the early Cretaceous. That the angiosperms may be polyphyletic is no new idea, and Wieland implies that geological evidence tends to support this view. Campbell (335) discusses this problem, and concludes that the weight of evidence appears to favour the view of Engler and Wettstein that the angiosperms are polyphyletic. He states that both comparative morphology and the geological record indicate that the existing angiosperms represent a

number of distinct phyla which cannot be traced back to a single ancestral type. The anatomical evidence appears to support this view.

SELECTED LITERATURE. (See also p. xxix)

Arber 30, Bailey 67, 68, 71, 75, Bailey and Sinnott 97, Bailey and Tupper 100, Bancroft 121, Barghoorn 137-9, Bews 193, Bliss 207, Bouvrain 247, Bremerkamp 267, Brown, F. B. H. 280, Campbell 335, Chalk 354, 357, Cheadle 382-8, Church 424, Coulter 483, Dormer 604, Eames 620, Frost 728-30, Gilbert 765, Hallier 874, Heimsch and Wetmore 939, Hill, T. G. 974, Hoar 981, Jeffrey 1162, 1163, 1168, 1169, Kostychev 1271, 1272, Kribs 1286, MacDuffie 1408, Majumdar 1426, Manning 1432, McNair 1473-8, Metcalfe 1500-2, Petersen 1706, Sinnott 2107, 2111, Sinnott and Bailey 2112, 2114, 2115, 2116, Smith, E. P. 2147, Stone 2204, Stopes 2208, Stopes and Fujii 2209, Tansley 2235, Thoday 2250, Thompson 2253-5, Thompson and Bailey 2256, Tippe 2261, 2263, 2264, Vestal 2329, 2330, Weiss 2392, Wieland 2421.

SELECTION AND PREPARATION OF MATERIAL

FOR all investigations in systematic anatomy it is essential to work with material that is accurately named. The ideal at which to aim is that all investigated material should be accompanied by herbarium specimens from the same plant. Since this ideal cannot always be attained, it is frequently necessary to compare specimens to be identified with museum samples. If the samples in the museum collections all agree with one another and have been obtained from reliable sources, identifications which are sufficiently accurate for practical purposes can usually be made, but it is desirable to compare material of which the identity has been established beyond question whenever possible. The difficulty of obtaining flowering specimens of commercial material is often very great, especially when it is customary for the flowers to be removed before the material is regarded as a commercial article. In consequence there are, even now, economic products of vegetable origin whose botanical identity has never been finally established in spite of their having been known in commerce for many years. It can thus be seen that the building up of collections of authentically named material for microscopical examination is of fundamental importance.

For general purposes, herbaceous material for microscopical examination is best fixed and preserved in formalin-acetic-alcohol or a similar solution until slides can be made. The taxonomist, when collecting specimens to be dried and mounted for the herbarium, would be doing a valuable service if he could also preserve material for anatomical work at the same time, since the authenticity of the material could then always be checked from the corresponding herbarium sheets. This would entail considerable additional labour on collecting expeditions, and might present difficulties in inaccessible localities, but modern transport facilities should make this easier as time goes on. Collections of floral material in fluid preserving media are now assuming increasing importance in herbaria, so it would be a logical development to include portions of the vegetative organs for anatomical investigation at the same time. Woody specimens can usually be preserved without any special treatment.

Herbarium specimens can frequently be revived sufficiently for their anatomical structure to be studied, but the ease with which this can be done

varies in different families. For example, revived specimens of the Solanaceae are usually most unsatisfactory. The usual procedure is to place the material in methylated spirit under reduced pressure to remove air from the tissues, after which it is transferred to hot water, which helps to soften it; then it is treated in cold dilute solutions of caustic soda or eau de Javelle, which frequently cause the cells to swell up and assume their original dimensions. The duration of treatment in each of the reagents, the gradual stages in passing from one to the other, and the strength of the caustic soda solution all need modification to suit the nature of the material. After the caustic soda treatment, the excess of alkali is neutralized with dilute acetic acid, the acid being subsequently removed by prolonged washing in running water. This treatment, or modifications of it, frequently enables material to be embedded in wax and sectioned on a microtome in the usual way, or good sections of relatively woody or rigid specimens may be cut on a sliding microtome without any preliminary embedding. Great care is necessary, however, when examining revived material, since the cells are not always fully restored to their original size and shape. This danger is apt to be especially great when revived material is compared with better-preserved specimens of the same species. Herbarium specimens are nearly always worth examining anatomically, but preference should be given to material preserved in a fluid medium.

Relatively hard material, such as wood, often needs no treatment other than boiling in water to remove the air. Very hard wood, however, may need softening. The most common methods of softening are by treatment with hydrofluoric acid, glacial-acetic acid with hydrogen peroxide, phenol under pressure, or a steam jet. Wood containing very thin-walled tissues, such as included phloem, or wood that is attacked by fungus, may need embedding in celloidin. A comprehensive account of the techniques of sectioning wood is given by J. Kisser (*Z. wiss. Mikr.* **48**, 320-42; 1932), and a briefer account of the most commonly used methods is given in the *For. Res. Leaflet*. No. 40; 1946. A critical comparison of different softening treatments is given by M. Harlow (*Tech. Publ. N.Y.S. Col. For.* **63**, 1944), and a more general description of sectioning, staining, &c., by C. J. Chamberlain (*Methods in Plant Histology*, Chicago, 1932). The acetic acid-hydrogen peroxide softening technique has been described by G. L. Franklin (*Trop. Woods*, **88**, 35-6; 1946).

The most common method of macerating wood is probably still that of Schultze, and consists of placing chips of wood in a test-tube with a few crystals of potassium chlorate and covering them with nitric acid diluted with its own volume of water. Another well-known method is to use a 5 per cent. solution of chromic acid. A newer technique, using glacial-acetic acid and hydrogen peroxide, has been described by G. L. Franklin (*Trop. Woods*, **49**, 21-2; 1937).

Another important requirement is to make reference collections of permanent microscope slides. These collections should be housed at institutions where taxonomic investigations are undertaken, especially at national herbaria. Permanent slide collections are as important for investigations in systematic anatomy as an ordinary herbarium collection is for taxonomic work based on external morphology. The lack of slide collections has done much to delay the development of systematic anatomy.

Arrangements for the exchange and loan of slides could be made with other institutions to the mutual advantage of all concerned. Work on these lines has already been accomplished in the restricted field of wood anatomy, extensive collections of authentically named timber slides having been assembled at a number of institutions in different parts of the world, including Great Britain. It is now desirable to extend these collections so as to include slides of other parts of the plant. In view of the magnitude of the task, attention should first be given to plants of economic importance or to those which are likely to assume economic importance. Sections of other plants could then be added gradually until a reasonably complete record of the anatomy of the higher plants has been secured. The slides should be filed in a logical sequence to facilitate easy reference, using a system which permits the collection to be expanded indefinitely without having to undertake its complete reorganization. This can easily be done in ordinary card index cabinets if the slides are arranged vertically in standard metal slide holders such as are now on the market. A filing system of this kind has considerable advantages over one in which the slides are arranged in boxes or cabinets of the usual type since far less space is required, and it is possible to add slides to the collection without having to rearrange all of them. At Kew the nucleus of a slide collection on these lines has been made during the last eighteen years, and has been found in practice to work efficiently and to save time when material is received for identification.

Examination under the microscope should not be confined to permanent slides. Certain features, such as bordered pits, are more clearly visible in sections mounted in dilute glycerine, whilst others, such as oily cell contents, are revealed by microchemical reagents whose effect is only temporary. Measurements of cells can best be made on macerated material, and clearing reagents often enable the course of vascular bundles to be seen, or sclerenchymatous idioblasts to be observed.

Samples of wood should always be selected from the main stem and not from branches. The very bottom of the stem should be avoided, even if there is no obvious swelling or buttressing, as the wood there is apt to be abnormal. Owing to the changes in cell dimensions that occur from the pith outwards at any given level, specimens should be located at some distance from the pith; a suitable position is often at the edge of the heartwood, with the specimen including both heartwood and sapwood, and it is useful to have the longest side of the specimen radial rather than tangential so as to include several growth rings. A convenient size is $4\frac{3}{4} \times 1 \times 6$ inches, or $8 \times 3 \times 15$ cm.

ARRANGEMENT OF THE FAMILIES

It was a matter of some difficulty for the authors to decide which system of classification should be used in the present book. On the advice of Sir Arthur Hill, who was the Director of Kew when the work was started, it was decided to arrange the families primarily in the sequence first introduced by Bentham and Hooker in their *Genera Plantarum*. It is generally recognized, however, that some of the families, as understood by Bentham and Hooker, do not constitute homogeneous units, for which reason many systematic botanists

have sought to improve the Bentham and Hooker classification either by regrouping genera so as to constitute new families or by elevating certain tribes or individual genera to family status. Many of the new families thus created have become generally accepted by qualified taxonomists and have been treated here as separate units. This procedure has greatly simplified the task of description.

In the following list the families in the left-hand column are those which were described by Bentham and Hooker in their *Genera Plantarum*. Those in the right-hand column are families that have since come to be generally accepted. In most instances the latter have been arranged in alphabetical sequence, following the Bentham and Hooker family in which the constituent genera of the new families were originally included. Thus, for example, the Ternstroemiaceae of Bentham and Hooker have become the Theaceae in a more restricted sense, together with nine families whose members were previously included in the Ternstroemiaceae as originally understood. A very few families, such as the Diclidantheraceae and Julianiaceae, have been removed from their positions in the Bentham and Hooker sequence, since this seems to be fully justified by the anatomical evidence. No claim is made that the families which follow one another closely in this sequence are nearly related in the true taxonomic sense. Some of them undoubtedly are, e.g. the families which constitute the Malvales. On the other hand, this is not true of others. For example, it is doubtful if the Hydrangeaceae (family 124) have any very close affinities with the Crassulaceae (family 125). In those families where the anatomical facts give some evidence of the true affinities of the families concerned, this has been indicated in the 'Taxonomic Notes' included in many of the family descriptions throughout the book. Until the taxonomic and phylogenetic interrelationships of the families are more fully understood, no arrangement can be entirely satisfactory. It is hoped, however, that the sequence of families that has been adopted will, with the aid of the index, facilitate easy reference, and at the same time avoid injuring the feelings of those taxonomists who have strong predilections for any other system.

I. POLYPETALAE

A. THALAMIFLORAE

RANALES

- | | |
|--------------------|----------------------|
| 1. Ranunculaceae | |
| 2. Dilleniaceae | |
| | 3. Crossosomataceae |
| 4. Calycanthaceae | |
| 5. Magnoliaceae | |
| | 6. Schisandraceae |
| | 7. Winteraceae |
| | 8. Cercidiphyllaceae |
| | 9. Eucommiaceae |
| | 10. Eupteleaceae |
| | 11. Himantandraceae |
| | 12. Lactoridaceae |
| | 13. Trochodendraceae |
| | 14. Tetracentraceae |
| 15. Annonaceae | |
| | 16. Eupomatiaceae |
| 17. Menispermaceae | |

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RANALES (<i>cont.</i>)	18. Berberidaceae	19. Circaeasteraceae
		20. Lardizabalaceae
		21. Sargentodoxaceae
	22. Nymphaeaceae ✓	
PARIETALES	23. Sarraceniaceae	
	24. Papaveraceae	
		25. Fumariaceae
	26. Cruciferae	
	27. Capparidaceae	
	28. Resedaceae	
	29. Cistaceae	
	30. Violaceae	
	31. Canellaceae	
	32. Bixaceae	
		33. Cochlospermaceae
	34. Flacourtiaceae (including Samydaceae)	
POLYGALALINAE	35. Pittosporaceae	
	36. Tremandraceae	
	37. Polygalaceae	
		38. Diclidanthaceae
	39. Vochysiaceae	
		40. Trigoniaceae
CARYOPHYLLINAE	41. Frankeniaceae	
	42. Caryophyllaceae (including Illecebraceae)	
	43. Portulacaceae	
	44. Tamaricaceae	
		45. Fouquieriaceae
GUTTIFERALES	46. Elatinaceae	
	47. Hypericaceae	
	48. Guttiferae	
		49. Quiinaceae
	50. Theaceae (including the anomalous genera <i>Clematoclethera</i> , <i>Sladenia</i> , and <i>Trematanthera</i>)	
		51. Actinidiaceae
		52. Bonnetiaceae
		53. Caryocaraceae
		54. Marcgraviaceae
		55. Medusagynaceae
		56. Pellicieraceae
		57. Pentaphylacaceae
		58. Saurauiceae
		59. Stachyuraceae
	60. Dipterocarpaceae	
		61. Ancistrocladaceae
	62. Chlaenaceae	
MALVALES	63. Malvaceae	
		64. Bombacaceae
	65. Sterculiaceae (including the Buettneriaceae)	
	66. Tiliaceae	
		67. Elaeocarpaceae
		68. Scytopetalaceae

B. DISCIFLORAE

GERANIALES

69. Linaceae

71. Humiriaceae

72. Malpighiaceae

73. Zygophyllaceae

74. Geraniaceae

70. Erythroxylaceae

75. Balsaminaceae

76. Limnanthaceae

77. Oxalidaceae

78. Tropaeolaceae

79. Rutaceae

80. Simarubaceae

81. Brunelliaceae

82. Cneoraceae

83. Koeberliniaceae

84. Ochnaceae (including *Strasburgeria*)

85. Tetrameristaceae

86. Burseraceae

87. Meliaceae

88. Dichapetalaceae (Chailletiaceae)

OLACALES

89. Olacaceae

90. Icacinaceae

91. Octoknemaceae

92. Opiliaceae

93. Aquifoliaceae (Ilicaceae)

94. Cyrillaceae

CELASTRALES

95. Celastraceae

96. Goupiaceae

97. Hippocrateaceae

98. Stackhousiaceae

99. Rhamnaceae

100. Ampelidaceae (Vitaceae)

SAPINDALES

101. Sapindaceae

102. Aceraceae

103. Akaniaceae

104. Hippocastanaceae

105. Melianthaceae

106. Staphyleaceae

107. Didiereaceae

108. Sabiaceae

109. Anacardiaceae

110. Corynocarpaceae

111. Julianiaceae

112. Coriariaceae

113. Moringaceae

C. CALYCIFLORAE

ROSALES

114. Connaraceae

115. Leguminosae

115A. Mimosaceae

115B. Caesalpinaceae

- ROSALES (cont.)**
- 117. Rosaceae
 - 118. Saxifragaceae
 - 125. Crassulaceae
 - 126. Droseraceae
 - 128. Hamamelidaceae
 - 131. Haloragaceae
- MYRTALES**
- 134. Rhizophoraceae
 - 135. Combretaceae
 - 136. Myrtaceae
 - 138. Melastomaceae
 - 139. Lythraceae
 - 144. Onagraceae (Oenotheraceae)
(Samydaceae incorporated in Flacourtiaceae)
- PASSIFLORALES**
- 145. Loasaceae
 - 146. Turneraceae
 - 147. Passifloraceae
 - 151. Cucurbitaceae
 - 152. Begoniaceae
 - 153. Datisceae
- FICOIDALES**
- 154. Cactaceae
 - 155. Ficoidaceae (Aizoaceae) (including Molluginaceae)
- UMBELLALES**
- 156. Umbelliferae
 - 157. Araliaceae
 - 158. Cornaceae
- 115C. Papilionaceae
 - 116. Krameriaceae
 - 117A. Rosaceae-Chrysobalanoideae
 - 119. Cephalotaceae
 - 120. Cunoniaceae
 - 121. Escalloniaceae
 - 122. Eucryphiaceae
 - 123. Grossulariaceae
 - 124. Hydrangeaceae
 - 127. Byblidaceae (Roridulaceae)
 - 129. Myrothamnaceae
 - 130. Bruniaceae
 - 132. Callitrichaceae
 - 133. Hippuridaceae
 - 137. Lecythidaceae
 - 140. Crypteroniaceae
 - 141. Oliniaceae
 - 142. Punicaceae
 - 143. Sonneratiaceae
 - 148. Achariaceae
 - 149. Caricaceae
 - 150. Malesherbiaceae
 - 159. Alangiaceae
 - 160. Garryaceae
 - 161. Nyssaceae

II. GAMOPETALAE

A. INFRAE

- RUBIALES**
- 162. Caprifoliaceae
 - 163. Adoxaceae
 - 164. Rubiaceae

ASTERALES

- 165. Valerianaceae
- 166. Dipsacaceae
- 167. Calyceraceae
- 168. Compositae

CAMPANULALES

- 169. Stylidiaceae
- 170. Goodeniaceae (including Brunoniaceae)
- 171. Campanulaceae
- 172. Lobeliaceae

B. HETEROMERAE

ERICALES

- 173. Vacciniaceae
- 174. Ericaceae
- 175. Clethraceae
- 176. Monotropaceae
- 177. Epacridaceae
- 178. Diapensiaceae
- 179. Lennoaceae

PRIMULALES

- 180. Plumbaginaceae
- 181. Primulaceae
- 182. Myrsinaceae (including Theophrastaceae)

EBENALES

- 183. Sapotaceae
- 184. Ebenaceae
- 185. Styracaceae
- 186. Symplocaceae

C. BICARPELLATAE

GENTIANALES

- 187. Oleaceae
- 188. Salvadoraceae
- 189. Apocynaceae
- 190. Asclepiadaceae
- 191. Loganiaceae
- 192. Gentianaceae

POLEMONIALES

- 193. Polemoniaceae
- 194. Hydrophyllaceae
- 195. Boraginaceae
- 196. Convolvulaceae (including Nolanaceae)
- 197. Solanaceae

PERSONALES

- 198. Scrophulariaceae
- 199. Orobanchaceae
- 200. Lentibulariaceae
- 201. Columelliaceae
- 202. Gesneriaceae
- 203. Bignoniaceae
- 204. Pedaliaceae (including Martyniaceae)
- 205. Acanthaceae

LAMIALES

- 206. Myoporaceae
- 207. Selaginaceae (including Globulariaceae)
- 208. Verbenaceae (including Phrymaceae)
- 209. Labiatae

III. MONOCHLAMYDEAE OR INCOMPLETAE

A. CURVEMBRYAE

- 210. Plantaginaceae
(Illecebraceae included in Caryophyllaceae)
- 211. Nyctaginaceae
- 212. Amaranthaceae
- 213. Chenopodiaceae
- 214. Basellaceae
- 215. Phytolaccaceae (including Achatocarpaceae and Gyrostemonaceae)
- 216. Batidaceae
- 217. Polygonaceae

B. MULTIOVULATAE AQUATICAE

- 218. Podostemaceae
- 219. Hydrostachyaceae

C. MULTIOVULATAE TERRESTRES

- 220. Nepenthaceae
- 221. Cytinaceae (Rafflesiaceae)
- 222. Hydnoraceae
- 223. Aristolochiaceae

D. MICEMBRYAE

- 224. Piperaceae
- 225. Saururaceae
- 226. Chloranthaceae
- 227. Myristicaceae
- 228. Monimiaceae

E. DAPHNALES

- 229. Lauraceae
- 230. Gomortegaceae
- 231. Hernandiaceae
- 232. Proteaceae
- 233. Thymelaeaceae
- 234. Gonystylaceae
- 235. Penaeaceae
- 236. Geissolomataceae
- 237. Elaeagnaceae

F. ACHLAMYDOSPOREAE

- 238. Loranthaceae
- 239. Santalaceae
- 240. Grubbiaceae
- 241. Myzodendraceae
- 242. Balanophoraceae

INTRODUCTION

G. UNISEXUALES

- | | |
|---|-----------------------|
| 243. Euphorbiaceae | 244. Buxaceae |
| | 245. Daphniphyllaceae |
| 246. Balanopsidaceae | |
| 247. Urticaceae | 248. Cannabinaceae |
| | 249. Cynocrambaceae |
| | 250. Moraceae |
| | 251. Ulmaceae |
| 252. Platanaceae | |
| 253. Leitneriaceae | |
| 254. Juglandaceae | |
| 255. Myricaceae | |
| 256. Casuarinaceae | |
| (Julianiaceae placed after Anacardiaceae) | |
| 257. Betulaceae | |
| 258. Corylaceae | |
| 259. Fagaceae | |

H. ANOMALOUS FAMILIES

260. Salicaceae
 261. Lacistemaceae
 262. Empetraceae
 263. Ceratophyllaceae

THE DESCRIPTIONS OF THE FAMILIES

THE descriptions of the individual families have, for the most part, been arranged according to the following plan. The system has been slightly modified for some of the families.

SUMMARY

- (i) GENERAL } A summary of the information given more fully under 'Leaf'
 (ii) WOOD } and 'Axis'.

LEAF

AXIS

(i) STEM

For woody plants this refers to stems of the first few seasons' growth or such as are to be found on herbarium sheets. For herbaceous plants, stems of all ages are dealt with in this section.

(ii) WOOD

This refers typically to the secondary xylem of mature stems large enough to produce timber, but the wood of small trees, shrubs, and lianes has also been described here if including the equivalent of several growth rings. The immature xylem, such as occurs in the first few seasons' growth, has been described separately under the section headed 'STEM'. For a complete picture of the secondary xylem, therefore, it is usually necessary to consult both of these sections.

(iii) ROOT

It has often been necessary to omit this section owing to the lack of information concerning the root structure of many families.

(iv) ANOMALOUS STRUCTURE

This section usually includes all the information about anomalous structure, but, where the anomaly known as included or interxylary phloem is characteristic of the secondary xylem of woody stems, this feature has generally been dealt with separately in the description of the wood, with a cross-reference in this section.

TAXONOMIC NOTES

The main object of this book has been to make anatomical data of taxonomic interest generally available, and no attempt has been made to provide solutions for all of the many taxonomic problems which have come to our notice. It was, however, felt that it would be useful to include in this section some notes on taxonomic conclusions drawn from anatomy by various investigators and recorded in the literature. This has been done, in most instances, without any additional comment from the authors. The authors have, however, expressed opinions of their own wherever original observations have made this appear desirable.

ECONOMIC USES

Since systematic anatomy can be and is generally applied in the identification of economic products, it seemed desirable to indicate the nature of the chief economic products derived from each family. It is hoped that the information included here, though necessarily far from complete, will prove useful to all who are concerned with the use of timber, as well as to students of economic botany, public analysts, pharmacognosists, and all who are concerned with the identification of fragmentary material of vegetable origin. For the wood, no attempt has been made to do more than show whether or not the family is important as a source of timber and indicate the most important species and genera.

GENERA DESCRIBED

At the end of most of the family descriptions there are two lists of the genera that have been included, one for the stem, root, and leaf, the other for the wood. Where the family is mainly or entirely herbaceous the second list has been omitted. In the first list an asterisk has been used to indicate that the genus is represented in the reference collection of microscope slides at Kew. In the list for the wood, brackets round a name indicate that no material of this genus was examined by the authors, but that information concerning at least some characters was available in the literature.

The inclusion of a genus in these lists does not necessarily mean that either the information or material available was fully representative, particularly in the case of genera with a large number of species, or that information was available on all of the characters included in the family description. The lists, however, should provide the reader with some indication of the extent to

which any particular family has been covered, and it is hoped that further research may be stimulated on those groups about which our knowledge is still rather meagre.

LITERATURE

Two separate lists are given at the end of most of the family descriptions, one for general anatomy and one for wood. Where the family is mainly or entirely herbaceous there is only one list. The numbers refer to the bibliography at the end of the book.

DESCRIPTIONS OF THE FAMILIES

1. RANUNCULACEAE

(FIG. 4 on p. 2; FIG. 7 on p. 14)

SUMMARY

(i) GENERAL

Mainly herbs, but including aquatic plants and some woody climbers. The family occurs mainly in the Northern Hemisphere, but extends into the tropics. The **vascular bundles**, in transverse sections, appear widely spaced, collateral, typically with the xylem concave on the side towards the phloem, so that the latter is often partly surrounded by xylem. Caps or arcs of fibres are present immediately on the outside of the phloem. A ring of **pericyclic sclerenchyma** is frequent in some genera, and in certain species the fibre groups adjoining the phloem are bounded externally by, or partly embedded in, the sclerenchymatous ring of the pericycle. In some genera, notably the Japanese species of *Ranunculus*, the vascular strands are entirely surrounded by sclerenchyma. **Xylem vessels** of herbaceous species have simple perforations, except in *Paeonia*, where scalariform plates have been recorded. **Medullary bundles** are usual in certain genera. **Petiole**, in transverse sections through the distal end, variable in outline, but always supplied by widely spaced vascular bundles arranged in an arc or circle or sometimes scattered. **Arm-palisade cells** are common in the leaf.

(ii) WOOD

Clematis

Vessels in tangential or irregular groups, ring-porous, with spiral thickening, perforation plates simple, intervacular pitting alternate, members of medium length to moderately short. **Parenchyma** paratracheal, storied. **Rays** all large, up to 12 or more cells wide and very high. **Fibres** with simple or bordered pits, storied, extremely short.

Paeonia

Vessels mostly solitary, ring-porous, perforation plates scalariform, intervacular pitting transitional and opposite, members of medium length. **Parenchyma** diffuse, very sparse. **Rays** up to 3 cells wide, with numerous uniseriata. **Fibres** with distinctly bordered pits, very short.

LEAF

Generally dorsiventral, rarely centric. **Hairs** including glandular and non-glandular types. Non-glandular trichomes mostly unicellular, of varied length. Simple, unicellular hairs recorded in *Thalictrum*. Small, unicellular, thin-walled, glandular hairs occur in *Adonis*, *Anemone*, *Aquilegia*, *Caltha*, *Clematis*, *Delphinium*, *Eranthis*, *Helleborus*, *Nigella*, *Ranunculus*, *Trollius*; glandular hairs with rather longer stalks observed by Solereder in *Helleborus* and *Ranunculus*. Cells of the lower **epidermis** with sinuous anticlinal walls; those of the upper epidermis generally straight. **Stomata** ranunculaceous;

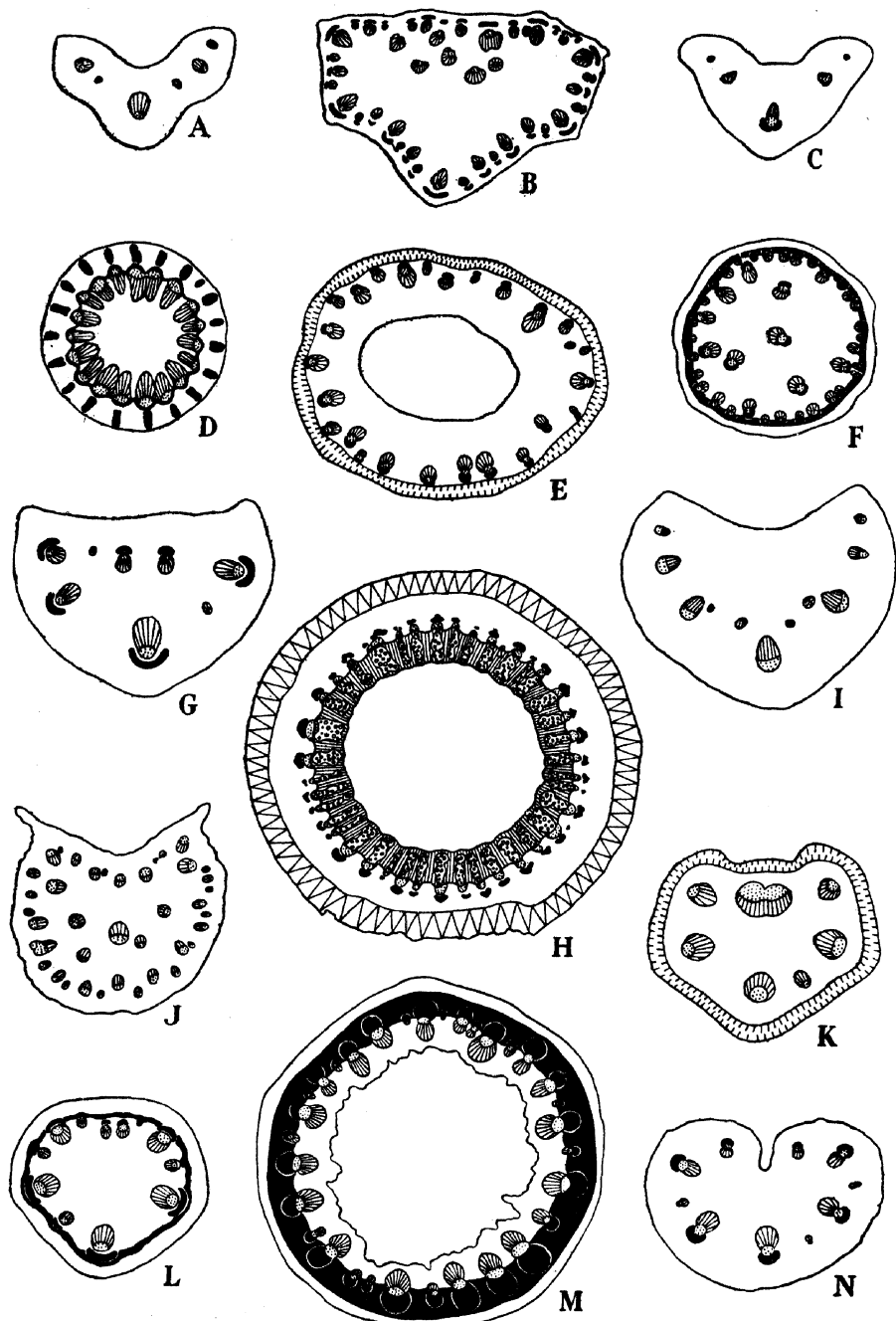


FIG. 4. RANUNCULACEAE

A, *Nigella integrifolia* Regel. Petiole $\times 8$. B, *Thalictrum 'rugosum'*. Petiole $\times 8$. C, *Adonis vernalis* Linn. Petiole $\times 28$. D, *Clematis afoliata* Buch. Stem $\times 10$. E, *Ranunculus acris* Linn. Stem $\times 10$. F, *Anemone vitifolia* Buch-Ham. Stem $\times 10$. G, *Aconitum 'gracile'*. Petiole $\times 19$. H, *Zanthoriza apifolia* L'Hérit. Stem $\times 13$. I, *Helleborus 'corsicus'*. Petiole $\times 8$. J, *Anemone vitifolia* Buch-Ham. Petiole $\times 8$. K, *Clematis vitalba* Linn. Petiole $\times 19$. L, *Aquilegia canadensis* Linn. Petiole $\times 19$. M, *Aconitum napellus* Linn. Stem $\times 10$. N, *Ranunculus acris* Linn. Petiole $\times 19$.

confined to the lower surface in some species, but present on both in others. (The list of genera in which these two types of stomatal distribution occur as given by Solereder probably needs revision and amplification according to Maue (1460), but the taxonomic value of the variations in this character appears to be somewhat limited.) Stomata of *Helleborus niger* Linn. described by Mühldorf (1568) as slightly below the general level of the epidermis, the guard cells being provided with cuticular teeth which become interlocked across the pores on closure. **Hydathodes** sometimes occur in association with the crenate teeth at the margins of the leaves. **Petiole** (Fig. 4 A-C, G, I-L, and N), in transverse sections through the distal end, exhibiting a considerable range of variations in outline, but nearly always provided with a number of widely spaced vascular bundles which may or may not be accompanied by pericyclic fibres according to the species. Petiolar vascular bundles arranged in a simple arc, e.g. in species of *Adonis*, *Helleborus*, *Nigella*; forming an almost or quite complete, sometimes adaxially flattened circle, e.g. in species of *Aconitum*, *Aquilegia*, *Clematis*, and *Ranunculus*; including a proportion of medullary petiolar bundles, e.g. in species of *Aquilegia* and *Thalictrum*. The petiolar structure might well afford characters of considerable diagnostic value if more completely investigated. Petiolar bundles of *Clematis flammula* Linn. not separate. (A study of 34 species and races of *Pulsatilla* by Zamels and Paegle (2502) showed the following leaf characters to be of taxonomic value. The presence or absence of a large ventral bundle in the petiole, and of a parenchymatous sheath around the individual bundles. Individual races and species are distinguishable by the amount and distribution of mechanical tissue and the number of bundles. On the basis of the first of these characters the genus may be divided into 4 groups.)

AXIS

STEM (Fig. 4 D-F, H, and M)

General topography of the aerial stem as indicated above under 'Summary'. **Cork** rarely formed, but known to be deep-seated in origin in a few woody species. **Vascular bundles**, in most genera and species, provided with xylem strands which are concave where adjoining the phloem, but outer boundary of the xylem flattened in *Paeonia*. Vessels of herbaceous species usually with simple perforations, but scalariform plates also occur in *Paeonia*. The primary vascular bundles usually remain widely spaced as seen in transverse sections, but the xylem of adjacent bundles becomes connected by fibres in the mature stem of species of *Paeonia*. **Interfascicular cambium** often absent from the woody genera *Clematis* and *Naravelia*, the bundles remaining separated by the primary rays, although secondary rays arise within the bundles. Secondary bundles originate from an interfascicular cambium in other species of *Clematis*. Additional rigidity is secured by thickening of the walls of the pith and cortex.

Vascular bundles frequently to be seen in transverse sections arranged in several circles, or more or less irregularly scattered; several circles present in *Actaea*, *Cimicifuga*, and *Thalictrum*; medullary bundles present in certain species of *Anemone*, *Anemonopsis*, *Delphinium*, *Glaucidium*, and '*Ranunculus*

chinensis'. A circle of medullary bundles extends from the base to the floral receptacle in the erect stem of *Glaucidium* (cf. Berberidaceae). The course of the medullary strands has been specially investigated by Kumazawa (1299) who recognized the following distinct arrangements. (i) Large leaf-trace strands becoming medullary at the nodes and gradually extending to the periphery; perianth strands not entering the pith. This type observed in species of *Anemonopsis*, *Delphinium*, *Thalictrum*, and in *Cimicifuga foetida* Linn. and '*Ranunculus chinensis*'. (ii) As (i) but perianth strands also entering the pith (*Anemone japonica* Sieb. & Zucc., *A. vitifolia* Buch-Ham., and *Glaucidium*). (iii) Leaf strands remaining at the periphery of the stem, but cauline bundles, and bundles from the lateral branches tending to be medullary in '*Cimicifuga japonica*'. The taxonomic value of vascular arrangements i-iii is unknown.

Pith generally parenchymatous, often with abundant intercellular spaces; becoming hollow in many herbs.

Clematis afoliata Buch, with reduced leaves, is provided with alternate bands of fibres and chlorenchyma in the cortex (Fig. 4 D).

Smith's (2146) examination of the stem anatomy in 138 species of *Clematis* has shown the general constructional scheme to be remarkably constant. Purely cauline bundles are absent throughout the genus, a starch sheath is generally present, and the periderm intrastelar in origin. Smith (2145) also found that vegetative propagation of *Clematis* by cuttings is facilitated by previous etiolation, because this causes mechanical softening of the tissues and restores the carbon-nitrogen ratio to the level that is necessary for meristematic activity. Fibres reduced in aquatic species of *Ranunculus*; schizogenous air passages being present on the inner side of the protoxylem. The nature of the interfascicular tissue and pericyclic sclerenchyma may be of specific diagnostic value. This has recently been confirmed for the species of *Ranunculus* which occur in Switzerland in a very detailed investigation by Bergman (185), who found that the amount and distribution of sclerenchyma in the pericycle and of fibre sheaths on the inner side of the vascular bundles afford valuable characters for the identification of species. Sheaths of sclerenchyma entirely surround the bundles in Japanese species of *Ranunculus*.

WOOD

Clematis (Fig. 7 A)

Vessels of the pore-zone large, those of the late wood small and in tangential or irregular groups; ring-porous; with spiral thickening (spiral thickening reported also (1851) in *Naravelia*). Perforations simple, horizontal in the larger vessels; MacDuffie (1408) describes some rare, irregular, multiperforate plates; imperfect vessels common. Intervascular pitting moderate-sized and alternate; pits to ray cells similar. Storied. Mean member length 0.25-0.5 mm. **Parenchyma** paratracheal, associated with the vessel groups. Fusiform strands common, strands otherwise of 2 cells. Storied. **Rays** all multiseriate, commonly up to 12 cells wide and sometimes many more; very high (more than 2 cm.); 1-2 per mm.; heterogeneous and with some sheath cells. **Fibres** with numerous, small, simple or bordered pits in both radial and tangential walls; walls moderately thin; storied; mean length 0.37-0.5 mm.

Paeonia

Vessels small and mostly solitary; ring-porous or semi-ring-porous; perforation plates scalariform, usually with 2-5 rather thick bars. Intervascular pitting transitional to opposite, pits to ray cells similar. Mean member length about 0.4 mm. **Parenchyma** limited to rare cells among the fibres. **Rays** up to 3 cells wide and less than 1 mm. high; with numerous uniseriataes; about 12 rays per mm.; composed entirely of square to upright cells. **Fibres** with numerous, conspicuously bordered pits in both radial and tangential walls. Walls thick. Mean length about 0.55 mm.

ROOTS AND RHIZOMES

Fleshy and fibrous roots occur in *Ranunculus*, cambium being scanty in or absent from the thin ones. Tuberous roots present in some species, e.g. *Aconitum* and *Ficaria verna* Huds. Ground tissue of the tubers chiefly consisting of the amyloiferous parenchyma of the cortex and sometimes the pith. According to Holm (1015, 1028), in *Aconitum uncinatum* Linn. and *Cimicifuga americana* Michx. the tuberous roots become thickened owing to the development of secondary bark.

In the tuberous roots of certain Indian species of *Aconitum* there are, according to Solereder, concentric vascular strands in the parenchymatous ground tissue of the central cylinder, each strand being provided with a pith, and growing in thickness by means of a partial cambium. These abnormal vascular strands arise from circular, secondary meristems situated in the pith, where they produce parenchyma and phloem towards the inside, and parenchyma and sometimes a few vessels on the outside. The secondary cambia subsequently become connected with the normal cambium. The rhizome of the xerophytic *Delphinium scaposum* Greene splits up into separate members during development. The accepted methods for distinguishing the rhizomes of *Helleborus niger* Linn. from those of *H. viridis* Linn. in use before 1924 are stated by Wallis and Saunders (2352) to be unreliable, but no alternative distinctive characters recorded. **Pith** of the mature root of *Ranunculus bullatus* Linn. described by Nicolas (1591) as becoming sclerenchymatous; the limited number of secondary xylem vessels arising by differentiation of cells of the conjunctive parenchyma. Contractile **exodermis** recorded in the roots of cultivated forms of *Anemone hepatica* Linn. **Berberin** present in the rhizome of *Coptis trifolia* Salisb. **Fungal hyphae** stated by Holm (1062) to be normally present in the roots of *Ranunculus bulbosus* Linn.

TAXONOMIC NOTES

The most interesting features of the herbaceous Ranunculaceae include the typical closed bundles with V-shaped xylem, and the frequent occurrence of several rings of or scattered bundles. These features suggest that the Ranunculaceae have close affinities with the Monocotyledons, especially the Alismataceae. In this connexion the monocotylous condition of *Ficaria verna* Huds. is significant. These and other facts indicate that the division of the angiosperms into Dicotyledons and Monocotyledons is not so absolute as has at times been supposed or implied. The vascular system of the Ranunculaceae

also shows affinities with that of some of the Berberidaceae. It has, in fact, been suggested on anatomical grounds by Kumazawa (1297) that certain genera of Berberidaceae and Ranunculaceae should be removed from their respective families and merged into a single family, the Podophyllaceae.

Worsdell (2469) has also drawn attention to the supposed anatomical affinities between *Paeonia* and the Magnoliaceae.

Worsdell's views were, however, based on rather slender evidence, and it is interesting to note that the resemblance between the secondary xylem of *Paeonia* and that of the Magnoliaceae is not very close. The most similar features are the scalariform perforation plates, but these indicate a similar level of specialization rather than affinity. In connexion with the low phylogenetic status which is commonly assigned to the Ranunculaceae, it is of interest that the wood of *Clematis* is of a moderately highly specialized type. It is also noteworthy that the wood of *Clematis* is not very similar to that of *Paeonia*.

ECONOMIC USES

The family includes well-known ornamental plants such as species of *Aconitum*, *Anemone*, *Clematis*, *Delphinium*, *Paeonia*, and *Ranunculus*. The Christmas Rose is *Helleborus niger* Linn.

Various members of the family are or have been used in medicine. One of the best known is Aconite Root, consisting of the dried tuberous roots of *Aconitum napellus* Linn. The conical roots are 4–10 cm. long when dried, and bear fibrous lateral roots or scars from which they have become detached. The pith appears stellate in transverse sections, and is bounded externally by a line of cambium which is more conspicuous than the xylem and phloem, the latter extending outwards to the endodermis, the cells of which have casparian thickenings. Other microscopical characters of diagnostic value include irregular, brown, tabular, suberized cells derived from the cortex which form a protective external layer; thick-walled, pitted sclereids in the cortex; 2–5 compound starch grains, the individual components being up to 30 (mostly 12–15) μ in diameter; absence of crystals and fibres. The roots of various other species of *Aconitum* are sometimes met with as substitutes or adulterants for those of *A. napellus*.

Cimicifuga or Black Snakeroot, also used in medicine, consists of the dried rhizomes and roots of *Cimicifuga racemosa* Nutt. obtained from North America. The horizontal rhizome, about 15 cm. long and 1–2 cm. in diameter, bearing, on the upper side, the bases or scars of stems and leaves, and brittle, often broken roots attached to the lower surface, the positions of detached roots being marked by scars. Microscopical features of the rhizome, visible in transverse sections, include numerous, narrow, triangular xylem groups separated by broad medullary rays; a cambium ring between the xylem and the thin, dark-coloured, horny bark; a dark-coloured pith; starch in all tissues except the xylem. In the root the 3–6 triangular xylem groups are united by their apices.

Black Hellebore, which was at one time used in medicine, consists of tortuous pieces of the rhizome of *Helleborus niger* Linn., characterized by cup-shaped scars of aerial stems, and root scars and roots 1–2 mm. thick attached to the lower surface. Transverse sections of the rhizome show a

wide cortex, surrounding a circle of 3–10 triangular xylem groups separated by wide medullary rays, the centre of the rhizome being occupied by a small brown pith. In each root there is a pale-yellow stele.

Seeds of *Nigella* and *Paeonia*, &c., have also been used in medicine.

The anatomy of the mildly poisonous *Ranunculus thora* Linn. has been described in some detail by Goris (797).

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aconitum,* *Actaea*,* *Adonis*,* *Anemone*,* *Anemonella*, *Anemonopsis*, *Aquilegia*,* *Cimicifuga*, *Clematis*,* *Coptis*, *Delphinium*,* *Glaucidium*, *Helleborus*,* *Hepatica*, *Isopyrum*, *Myosurus*,* *Naravelia*, *Nigella*,* *Paeonia*,* *Pulsatilla*, *Ranunculus*,* *Thalictrum*,* *Trollius*,* *Zanthoriza*.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Clematis, (*Naravelia*), *Paeonia*.

LITERATURE

(i) *On General Anatomy*

Bergman 185, Betts 187, Bird 199, Bretin 268, Crockart 502, Giersch 764, Goris 797, Holm 996, 997, 1015, 1029, 1050, 1062, 1068, Kingsley 1237, Kumazawa 1297, 1299, 1300, Maue 1460, Munch and Crosby 1574, Mühldorf 1568, Nicolas 1591, Rabbas 1769, Salisbury 1984, Smith, E. P. 2145, 2146, Wallis and Saunders 2352, Worsdell 2469, Zamels and Paegle 2502.

(ii) *On Wood Structure*

Dadswell and Record 533, MacDuffie 1408, Pfeiffer, H. 1712, Record 1843, 1851.

2. DILLENiaceae

(FIG. 5 on p. 8; FIG. 6 on p. 12; FIG. 8 on p. 20)

SUMMARY

(i) GENERAL

A family of trees, shrubs, climbers, or, more rarely, herbs, which occurs in tropical and subtropical regions. The **hairs** are simple, unicellular trichomes or stellate; glandular types absent. The **stomata** are usually ranunculaceous, except in *Tetracera*. **Crystals** of calcium oxalate occur chiefly in the form of raphides, but transitional forms between these and crystal-sand have been recorded in *Curatella*, *Davilla*, *Dillenia*, and *Doliocarpus*. Canals containing crystal-sand have also been observed in certain members of the family, and tetrahedral crystals are present in the phloem of the leaf veins and axis as well as in the mesophyll of *Hibbertia scandens* (Willd.) Gilg. These are absent from other members of the genus.

(ii) WOOD

Vessels solitary, perforation plates scalariform, or simple and scalariform, intervacular pitting opposite to scalariform, members moderately to extremely long. **Parenchyma** predominantly apotracheal, diffuse or in uniseriate lines, with a few cells about the vessels; sometimes containing raphides. **Rays**

8–10 cells wide or more and high, heterogeneous, sometimes containing raphides. **Fibres** with distinctly bordered pits, moderately to very long. **Anomalous structure** of the banded type present in *Doliocarpus*.

LEAF

Mostly dorsiventral with 1–4 layers of palisade tissue, but centric or sometimes ericoid, with furrows on the lower side, in certain members of the

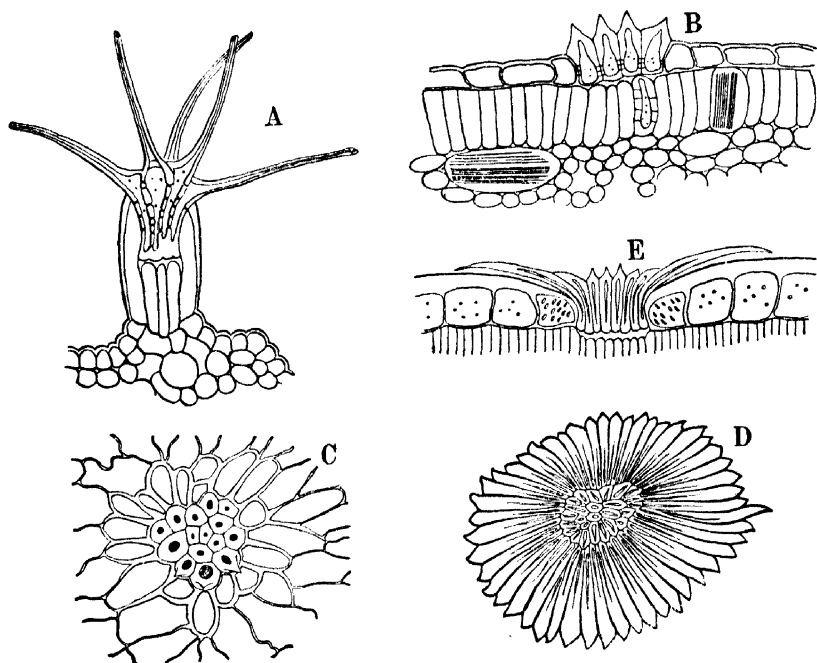


FIG. 5. DILLENIACEAE

A, stellate hair of *Hibbertia furfuracea* (R. Br.) Benth. B–C, spiny hair of *Tetracera oblongata* DC.: B, transverse section through the spiny hair and through a piece of leaf-tissue. C, surface view of the spiny hair with the surrounding cells of the upper side of the leaf. D–E, peltate hair of *Hibbertia lepidota* R. Br.: D, in surface view; E, in section.—By Solereder.

Hibbertieae from dry habitats in Australia. Expansion of the leaf is controlled by specialized motor tissue at the margin in *Hibbertia rhadinopoda* F. v. Muell. The leaves of other species of *Hibbertia* from more humid regions exhibit typical dorsiventral structure. **Hairs** (Fig. 5 A–E) in the form of simple, unicellular trichomes, or stellate; the stellate hairs and scales most numerous in the xeromorphic Hibbertieae. Peltate scales also recorded in *Hibbertia lepidota* R. Br. **Epidermis** often silicified. **Stomata** usually ranunculaceous, but rubiaceous in *Tetracera oblonga* DC.; generally level with the surface of the leaf, although sunken in xeromorphic Hibbertieae, especially in the phylloclades of *Pachynema*. **Hypoderm** recorded in certain species of *Wormia* and in *Dillenia indica* Linn. Sclerenchymatous **idioblasts** said to be present in *Hibbertia grossulariaefolia* Salisb. and *H. linearis* R. Br. **Midrib** containing a closed ring of vascular bundles in *Curatella*, *Davilla*,

Doliocarpus, and *Tetracera*, but with 2-7 or more concentric bundles in *Acrotrema* and *Dillenia* or a circle of collateral bundles in the midrib of *Schumacheria*. **Petiole** of *Dillenia indica* (Fig. 6 A), in transverse sections through the distal end, exhibiting a closed, cylindrical vascular strand accompanied by subsidiary bundles in the wings. A wide crescent-shaped strand with a smaller dorsal one between the arms present in the corresponding position in *Hibbertia volubilis* Andr. (Fig. 6 C). All leaf tissues turn brown when dried owing to the presence of tanniniferous substances. **Crystals**. Raphides situated in elongated, often thick-walled, sacs or tubes, present in the mesophyll and in the phloem of the veins. Similar sacs or tubes sometimes filled with crystal-sand, or types of crystal intermediate between raphides and crystal-sand.

AXIS

YOUNG STEM (Fig. 6 B)

Cork deep-seated in origin in species of *Davilla*, *Doliocarpus*, *Hibbertia*, and *Tetracera*; sub-epidermal in *Dillenia*. Cork cells of *Dillenia pentagyna* Roxb. with thin walls, but in other species and genera usually with thicker walls. **Pericycle** generally including a continuous ring of sclerenchyma except in *Acrotrema*, species of *Hibbertia* and *Tetracera scandens* (Forst.) Gilg et Werd. At first continuous, but becoming broken in *Dillenia indica* Linn. **Xylem** traversed by broad rays in *Dillenia indica* and by less frequent broad rays in *Hibbertia volubilis* Andr.; containing vessels of very variable diameter depending on the habit of the plant. Vessels mostly with scalariform perforation plates, although these sometimes become simple owing to the destruction of the bars, notably in *Davilla* and *Tetracera* (see also Wood below). **Pith** generally containing elongated, sclerenchymatous idioblasts with white inclusions in *Davilla*, *Doliocarpus*, and *Tetracera*; generally septate in *Wormia*; including groups of stone cells in *Curatella*, *Davilla*, *Dillenia*, *Doliocarpus*, and *Tetracera*. Raphides, crystal-sand, and transitional forms of **crystals** present in elongated sacs or canals in all unligified parts of the stem, notably in the cortex, phloem, and pith.

WOOD (Fig. 8 I, J, L)

Vessels usually medium-sized (mean tangential diameter 100-200 μ), large (more than 200 μ) in the lianes, e.g. in *Davilla* and *Doliocarpus*; exclusively solitary, except for apparent tangential pairs due to overlapping ends; usually 1-8 per sq. mm., but, according to Vestal (2329), sometimes up to 50 per sq. mm. Perforation plates typically scalariform, with few to numerous bars (up to 130), though sometimes accompanied by simple perforations; perforations mostly simple in *Davilla*, *Doliocarpus*, and *Tetracera* (2329), but with some scalariform plates in the smaller vessels. Intervascular pitting rare except in the overlapping end-walls, opposite to scalariform. Often filled with yellow to white chalky contents; tyloses reported (2329) in *Dillenia*; Gonggrijp (794) has observed silica in *Dillenia* and *Wormia*. Mean member length 0.7-2.0 mm. **Parenchyma** predominantly apotracheal, as scattered cells (diffuse) or short, uniseriate tangential lines (Fig. 8 L), the lines more continuous in *Curatella*; often with a tendency to form incomplete

sheaths round the vessels (Fig. 8 j); cells often filled with gum-like substance. Enlarged cells containing raphides present in some species of *Dillenia* and in the conjunctive tissue of *Doliocarpus*. Strands usually of 8 cells. **Rays** usually of two distinct sizes, the larger commonly up to 8–10 cells wide and up to 20 or more cells wide in *Curatella* and *Davilla*, but all narrow, according to Tupper, in *Acrotrema*, *Hibbertia*, and *Pachynema*; commonly more than 2 mm. high; uniseriates numerous and composed of upright cells; 4–12 rays per mm.; heterogeneous (Kribs's Types I and II A), with 4–10 (occasionally more) marginal rows of square to upright cells; with square and procumbent cells intermingled in *Curatella* and *Davilla*, and, to a less extent, in *Wormia*. Raphides present in enlarged mucilage cells (Fig. 8 i) in *Curatella*, *Dillenia* (lacking from *D. aurea* Smith (1154)), *Tetracera* (959), and *Wormia*. Scleroid cells reported (2329) in *Davilla*. **Fibres** with distinctly bordered pits on both radial and tangential walls, the pits very large in *Doliocarpus*. Walls thin to moderately thick. Mean length 1.8–3 mm. **Included (interxylary) phloem** of the concentric type (*C. l. circumvallatum*) present in *Doliocarpus*, the short-lived cambium being periodically replaced by new meristematic tissue, which repeats the structure of the young stem.

ANOMALOUS STRUCTURE, *see under* 'WOOD'

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Actinidia, *Clematoclethra*, *Saurauia*, *Sladenia*, *Trematanthera* resemble both the Dilleniaceae and the Theaceae. This is of interest because, as Hutchinson (1113) has pointed out, there are affinities between the Dilleniales and Theales. For this reason it has been difficult to decide on the most appropriate position for the inclusion of the above genera in this book. Since Actinidiaceae and Saurauiaceae are commonly recognized as distinct families, the single genus included in each has been described under these family names. *Clematoclethra*, *Sladenia*, and *Trematanthera*, whose position is less well established, have been provisionally described as anomalous genera under Theaceae. It is interesting to note that Beauvisage (163) expressed the view that the anatomical characters in general, and in particular those of the petiole, combined with the presence of raphides, suggest that the affinities of all of the above genera lie closer to the Dilleniaceae than to the Theaceae.

(ii) FROM WOOD STRUCTURE

Vestal (2329) notes that there is little difference in anatomy between members of this family and those of the Actinidiaceae, Saurauiaceae, and Theaceae. Bausch (154) found that the anatomy of the wood shows no very close relation to that of the Eucryphiaceae.

ECONOMIC USES

The silicified cells on the surface enable the leaves of *Tetracera* to be used in the same way as sand-paper for polishing wood.

Some of the species of *Dillenia* provide timbers that are used locally for general construction and boat-building, and occasionally for furniture.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acrotrema, Curatella, Davilla, Dillenia,* Doliocarpus, Hibbertia,* Pachynema, Schumacheria, Tetracera, Wormia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Acrotrema), Curatella, Davilla, Dillenia, Doliocarpus, (Hibbertia), (Pachynema), (Schumacheria), (Tetracera), Wormia.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Gilg and Werdermann 781, Hutchinson 1113, Kastory and Namylovsky 1223, Lechner 1328, Shelton 2086, Solereder 2165, Thompson 2254.

(ii) *On Wood Structure*

Bausch 154, den Berger 179, 182, Chalk and Chattaway 362, Dadswell and Record 533, Desch 574, Foxworthy 704, Gonggrijp 794, Hess 959, Howard 1088, Janssonius 1154, Kanehira 1206, Lechner 1328, Lecomte 1334, Pearson and Brown 1679, Pfeiffer, H. 1712, Record 1843, 1851, Record and Hess 1886, Record and Mell, 1894, Tupper 2295, Vestal 2329, Williams 2430.

3. CROSSOSOMATACEAE

(FIG. 6 on p. 12)

SUMMARY

The sole representatives of this family are the Californian shrubs belonging to the genus *Crossosoma*. The following description of the leaf and stem is based chiefly on fresh material grown at Kew. The wood exhibits the following features: **Vessels** very small, ring-porous, perforations simple, intervascular pitting alternate. **Parenchyma** sparse, paratracheal. **Rays** up to 6 cells wide, heterogeneous. **Fibres** with large bordered pits.

LEAF

Isobilateral, the component cells containing small, dark-coloured bodies of unknown nature. **Epidermis** composed of cells with sinuous anticlinal walls. **Stomata** present on both surfaces but most numerous on the lower side; ranunculaceous. **Petiole** (Fig. 6 E), in transverse sections through the distal end, exhibiting an open arc of separate collateral bundles, not accompanied by fibres in the pericyclic region. Vessels of the petiolar bundles in radial rows. No raphides, crystalliferous sacs, or tubes present, but small rosettes or dendritic groups of minute acicular **crystals** present in some of the epidermal cells on both surfaces.

AXIS

YOUNG STEM (Fig. 6 H)

Cork arising at a very early stage in the sub-epidermal region. Primary **cortex** parenchymatous. **Pericycle** containing small, very narrow strands of thick-walled fibres. **Phloem** devoid of sclerenchymatous elements. **Xylem** forming an almost continuous cylinder, traversed by fairly narrow but lignified, primary medullary rays; including vessels up to about 20 μ in

diameter, arranged in radial rows, and provided with minute bordered pits and simple perforations. **Pith** composed of abundantly pitted parenchymatous cells; occasionally hollow. Minute, yellow, acicular **crystals** closely

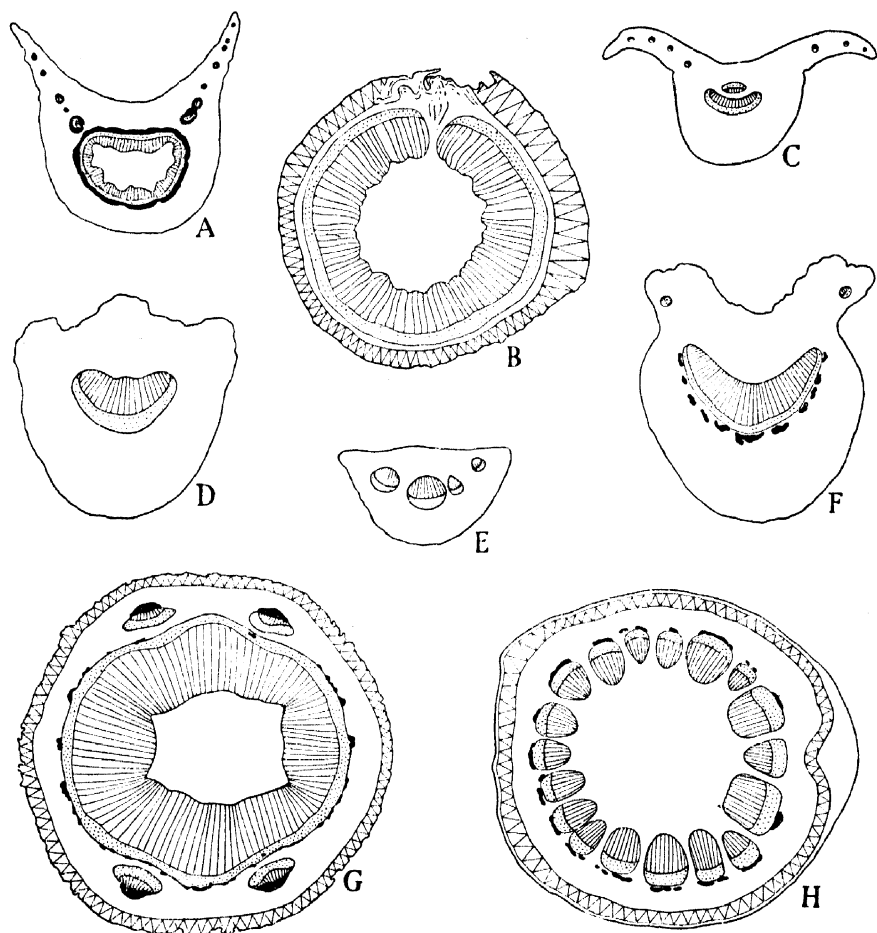


FIG. 6. *DILLENIACEAE*, A-C; *CALYCANTHACEAE*, D, F, and G; *CROSSOSOMATACEAE*, E and H

A, *Dillenia indica* Linn. Petiole $\times 8$. B, *Hibbertia volubilis* Andr. Stem $\times 13$. C, *H. volubilis* Andr. Petiole $\times 8$. D, *Chimonanthus fragrans* Lindl. Petiole $\times 19$. E, *Crossosoma californicum* Nutt. Petiole $\times 27$. F, *Calycanthus floridus* Linn. Petiole $\times 19$. G, *C. occidentalis* Hook. et Arn. Stem $\times 19$. H, *Crossosoma californicum* Nutt. Stem $\times 27$.

packed in clusters of cells in the phloem. (These crystals are entirely unlike the raphides and crystal-sand which occur in the phloem throughout the Dilleniaceae.)

WOOD¹

Vessels small to minute (15–55 μ) and angular, those of the latewood solitary, but grouped into radial rows by the rays; ring-porous. Perforations

¹ Based on the description by Record and Hess (1886).

simple. Intervascular pitting alternate and small, pits to ray cells similar. Many very small vessels with 'fibriform members'. **Parenchyma** sparse, paratracheal. **Rays** up to 6 cells wide; heterogeneous, with most of the cells square or upright and the procumbent cells short. **Fibres** with numerous, large-bordered pits and thick walls, scarcely distinguishable from the fibriform vessel members.

TAXONOMIC NOTES

The absence from *Crossosoma* of raphides as well as of tubes or sacs filled with raphides or crystal-sand is a clear indication that the genus has no close affinities with the Dilleniaceae.

GENUS DESCRIBED
(*Crossosoma**)

* Represented in the Kew slide collection.

LITERATURE

On Wood Structure. Record 1843, 1851, Record and Hess 1886.

4. CALYCANTHACEAE

(FIG. 6 on p. 12; FIG. 7 on p. 14)

SUMMARY

(i) GENERAL

Shrubs from North America and the Far East. The most distinctive anatomical feature of the young stem of this family is the presence of 4 inversely orientated vascular bundles in the pericycle (Fig. 6 g). **Secretory cells** are present. **Hairs** unicellular; surrounded by silicified cells. The **stomata** are rubiaceous. The **cork** in the axis arises in the sub-epidermis, and the first-formed periderm cells are radially elongated. The bark cells are stated by Quinlan (1767) to be pitted.

(ii) Wood

Vessels very small, with a marked oblique or flame-like pattern, ring-porous, with spiral thickening, perforations simple, intervacular pitting alternate and large; members moderately short to medium-sized. **Parenchyma** limited to a few cells round the vessels. **Rays** up to 4 cells wide and composed almost entirely of square and upright cells. **Fibres** with simple or small-bordered pits, very to moderately short.

LEAF

Dorsiventral. Bases of the unicellular **hairs** surrounded by a rosette of cells with silicified walls, having the appearance of dark or translucent dots in dried specimens. **Stomata** rubiaceous; confined to the lower surface. **Mesophyll**. Palisade tissue indistinct in *Calycanthus floridus* Linn. **Petiole** of *Chimonanthus fragrans* Lindl. (Fig. 6 d), in transverse sections through the distal end, exhibiting a single, slightly arc-shaped vascular strand; that of *Calycanthus floridus* Linn. (Fig. 6 f) provided with a larger and rather more invaginated median vascular arc, accompanied by small accessory strands in

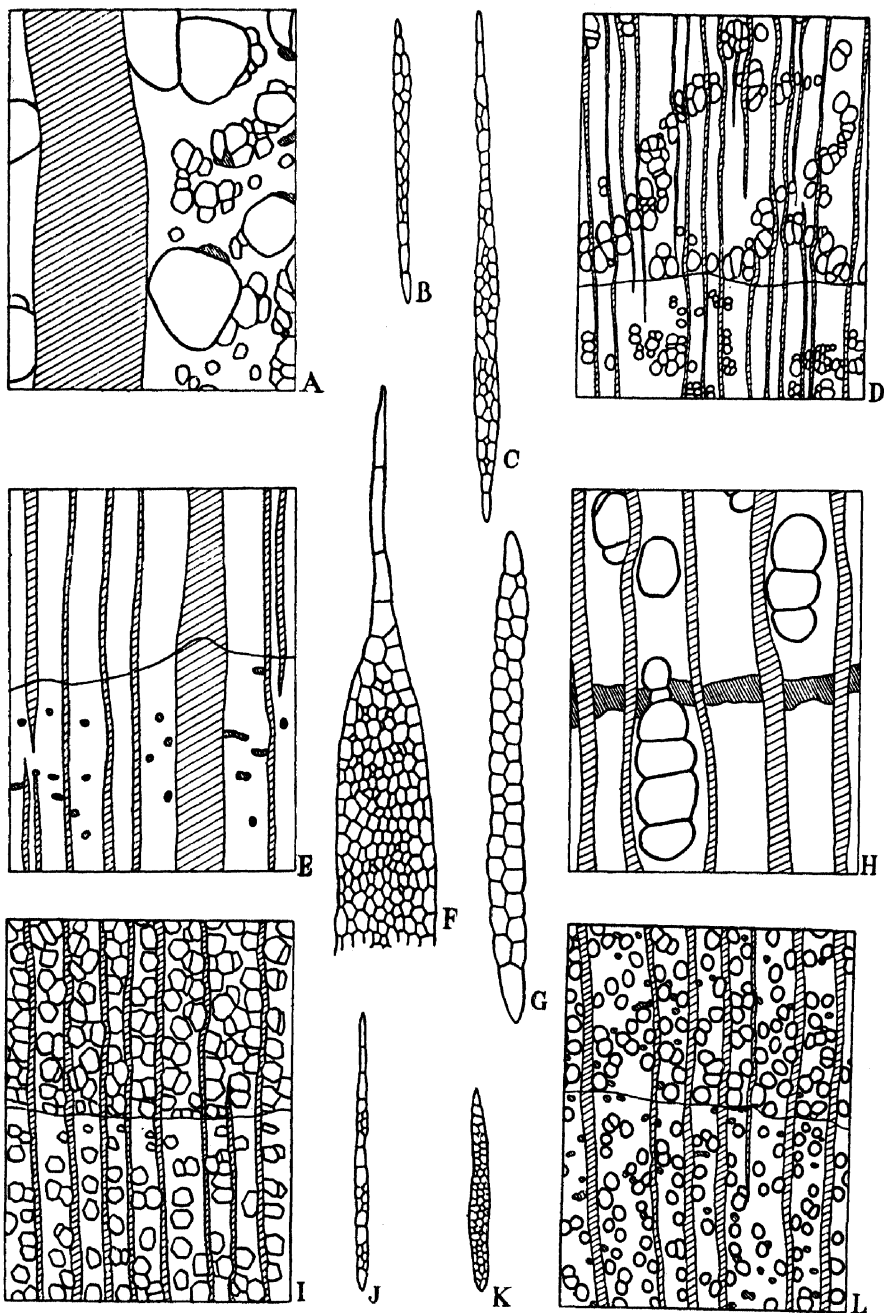


FIG. 7. *RANUNCULACEAE*, A; *CALYCANTHACEAE*, B-D; *TROCHODENDRACEAE*, E-F; *HIMANTANDRACEAE*, G-H; *CERCIDIPHYLLACEAE*, I-J; *EUCOMMIACEAE*, K-L

A, *Clematis vitalba* Linn. T.S. B, *Calycanthus floridus* Linn. Ray. C, *Chimonanthus fragrans* Lindl. Ray. D, *Calycanthus floridus* Linn. T.S. E, *Trochodendron aralioides* Sieb. et Zucc. T.S. F, *T. aralioides* Sieb. et Zucc. Ray. G, *Himantandra belgraveana* Diels. Ray. H, *H. belgraveana* Diels. T.S. I, *Cercidiphyllum japonicum* Sieb. et Zucc. T.S. J, *C. japonicum* Sieb. et Zucc. Ray. K, *Eucommia ulmoides* Oliv. Ray. L, *E. ulmoides* Oliv. T.S.

the wings. **Secretory elements.** Secretory cells present in the mesophyll or lower epidermis. Oil cells, chiefly present in the veins, but to a smaller extent in the mesophyll in *Calycanthus floridus*, according to Lehmann (1343).

AXIS

YOUNG STEM (Fig. 6 G)

Four **pericyclic bundles** (leaf traces), with external xylem and internal phloem, present in *Calycanthus* and *Chimonanthus*. Pericycle including a continuous ring of sclerenchyma in the lower nodes of *Chimonanthus*. Isolated strands of fibres situated in the corresponding position in *Calycanthus*. Pericyclic fibres and stone cells showing U-shaped thickenings in longitudinal sections. **Xylem**, in transverse sections, appearing as a continuous cylinder traversed by narrow rays. **Pith** consisting of thin-walled parenchyma. **Oil cells** present in the parenchymatous portions of the axis.

(The distinction recorded by Solereder that the external bundles of *Calycanthus* consist of undivided vascular strands in the cortex, whereas the corresponding bundles in *Chimonanthus* are double strands in the pericycle, was not substantiated by direct observation. In both genera the pericyclic bundles are bounded externally by groups of fibres which appear to be continuous with the pericyclic sclerenchyma. Nor could the 'double' nature of the strands in *Chimonanthus* be confirmed.)

WOOD (Fig. 7 B-D)

Vessels very small (25–50 μ mean tangential diameter), often little wider than the fibres and angular in cross-section; in clusters and radial pore-multiples that are grouped to give a distinct oblique or 'flame-like' pattern, very numerous; ring-porous, or semi-ring-porous; with spiral thickening. Perforations simple, oblique; imperfect vessel members common. Intervascular pitting alternate and large, the apertures round in *Calycanthus*. Pits to ray cells usually similar to the intervacular pitting in size and shape, but occasionally larger and irregular in shape; simple. Mean member length about 0.3 to 0.4 mm. **Parenchyma** very scanty; paratracheal, consisting of a few cells around the vessels. Garratt (747 A) refers also to diffuse parenchyma in *Calycanthus*, but this was not observed by the author. **Rays** small and low, except for some wider and higher rays in *Chimonanthus* that appear to have been dissected out from large primary rays. 1–2 (occasionally 3) cells wide in *Calycanthus*, 1–3 (occasionally 4) cells wide in *Chimonanthus*; composed almost entirely of square or upright cells with few truly procumbent cells; with about 4 uniseriate marginal rows in *Calycanthus* and up to 8 rows in *Chimonanthus*. Perforated ray cells very common (358). Uniseriate rays numerous, often only 1–2 cells high; of mixed square and upright cells, as in the multiseriate rays. **Fibres** with small pits mostly on the radial walls, with small borders in *Calycanthus*; walls thin; mean length about 0.7 mm. **Vasicentric tracheids** with spiral thickening present in both genera.

TAXONOMIC NOTES

The Calycanthaceae in the Bentham and Hooker system were placed in the Ranales between the Dilleniaceae and Magnoliaceae, similarities to the Rosaceae, Combretaceae, and Monimiaceae also being mentioned. In the

Engler system the family is likewise placed near the Magnoliaceae, whereas Hutchinson (1113), includes them in the Rosales, thus recognizing their affinities with the Rosaceae and Dichapetalaceae. In this connexion it is interesting to record Tippo's (2261) somewhat guarded view based on the anatomical characters of the wood, 'that the derivation of the Calycanthaceae from the more primitive members of the Rosaceae would be inconsistent with the anatomical facts'. He also draws attention to features in which the Calycanthaceae resemble the Himantandraceae and Lactoridaceae which are included in the Magnoliales.

Garratt (747 A) says: 'The Calycanthaceae have very few anatomical features in common with the great majority of Monimieae genera and the points of distinction are so outstanding as to indicate that their relationship, if any exists, is remote. Only with *Bracteanthus*, *Peumus*, and *Siparuna* is there sufficient similarity to the Calycanthaceae to indicate possible, although somewhat indefinite, affinity.'

According to Record and Hess (1886) the 'Structure does not suggest that of the order Rosales'.

ECONOMIC USES

Carolina Allspice (*Calycanthus floridus* Linn.) has an aromatic bark.

GENERA DESCRIBED

Calycanthus,* *Chimonanthus*.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113, Lehmann 1343, Quinlan 1767, Tison 2265, Worsdell 2469.

(ii) *On Wood Structure*

Chalk and Chattaway 358, Garratt 747A, Record 1843, 1851, Record and Hess 1886, Tippo 2261.

5. MAGNOLIACEAE

(FIG. 8 on p. 20; FIG. 10 on p. 32)

SUMMARY

(i) GENERAL

Trees and shrubs, now with a comparatively restricted distribution in parts of North America, the West Indies, Brazil, the Far East, India, and Malaya, &c. The geological record shows that the family was at one time much more widely distributed in the Northern Hemisphere. **Stomata** are usually confined to the lower surface of the leaf. In the stem the **cork** arises in the epidermis, hypodermis, or outer part of the cortex. Complete or incomplete diaphragms of stone cells are common in the broad pith. **Secretory cells** with mucilaginous or oily contents are very frequent, especially in parenchymatous tissues. Calcium oxalate, when present, occurs as small octahedral or prismatic **crystals**.

(ii) Wood

Vessels solitary and in small groups, sometimes with spiral thickening, perforation plates typically scalariform with few, widely spaced bars, but simple perforations often present and sometimes predominant, intervacular pitting scalariform to opposite, members moderately long. **Parenchyma** terminal only. **Rays** usually up to 3 or 4 cells wide, with few uniseriatae, heterogeneous to homogeneous, sometimes with oil cells. **Fibres** with bordered pits, of medium length to very long.

LEAF

Usually dorsiventral. **Hairs** mostly uniseriate, multicellular, but sometimes unicellular in *Magnolia* and *Michelia*. Tufted hairs with 1- or 2-celled rays recorded in *Michelia* spp. **Epidermis** composed of cells with straight or sinuous anticlinal walls; outer walls sometimes striated or covered with granular deposits of wax. Epidermis silicified, e.g. in *Magnolia grandiflora* Linn. and *M. virginiana* Linn.; papillose in *Liriodendron tulipifera* Linn., *Magnolia ferruginea* Parm., and *Michelia punduana* Hook. f. et Thoms. **Hypoderm** present below the upper epidermis in *Liriodendron tulipifera*, *Magnolia* spp., *Manglietia insignis* Bl., *Michelia* spp., and *Talauma ovata* St. Hil. A second layer of cells, similar to those of the hypoderm, present beneath the palisade layers in *Liriodendron tulipifera* according to Holm (1936). **Stomata** usually confined to the lower surface; mostly rubiaceous, but sometimes ranunculaceous types present as well, e.g. in *Liriodendron*. **Petiole** (Fig. 10 A, C, G, and I), in transverse sections through the distal end, exhibiting a circle of separate collateral bundles in *Liriodendron*, *Magnolia*, *Michelia*, and *Talauma*. One of the bundles in the base of the petiole of *Liriodendron* tending to become medullary. Bundles scattered in the base of the petiole of *Talauma hodgsoni* Hook. f. et Thoms. according to Worsdell (2469). Ozenda (1645, 1647) has recently drawn attention to the numerous vascular strands in the base of the petiole of various members of the Magnoliaceae. (See also ANNONACEAE under 'Petiole' for similar structure in *Uvaria*.) **Secretory cells**, sometimes with suberized walls, common in parenchymatous tissues. The mode of development of the oil cells in *Liriodendron* and *Magnolia* has been described by Lehman (1943).

AXIS

YOUNG STEM (Fig. 10 B)

Cork superficial, generally arising in the sub-epidermis. Primary **cortex** including groups of stone cells and/or branched sclerenchymatous idioblasts in *Magnolia*, *Manglietia*, and, according to Holm (1936), in *Liriodendron*. **Phloem** strands in *Liriodendron tulipifera* Linn. each bounded externally by a cap of fibres; fibres also occurring but forming less definite caps at the periphery of the phloem in species of *Magnolia* examined at Kew. Secondary phloem sometimes including concentrically arranged strands of fibres. **Xylem** and phloem of adjacent vascular strands in *Liriodendron* and *Magnolia* usually sufficiently separated by conspicuous, primary medullary rays to appear as distinct vascular bundles in transverse sections. Vessels frequently

with scalariform perforation plates. **Pith** generally broad; often divided by transverse septa composed of sclerenchymatous cells. **Secretory cells** common in parenchymatous tissues.

WOOD (Fig. 8 A-B, E-G, and K)

Vessels usually medium-sized (mean tangential diameter 100–200 μ), but small (less than 100 μ) in *Alcimandra*, *Liriodendron*, *Magnolia*, *Manglietia*, and *Michelia* p.p.; solitary, in short radial multiples and in occasional clusters; radial multiples moderately pronounced in *Elmerillia* and *Liriodendron*; very variable in number, 5–100 per sq. mm.; most numerous in *Liriodendron* and *Magnolia*, and fewest in *Aromadendron* and *Elmerrillia* p.p., e.g. *E. mollis* Dandy; spiral thickening observed or reported (1467, 1851) in *Alcimandra*, *Aromadendron*, *Magnolia*, *Michelia*, and *Talauma* (1851). Perforation plates typically scalariform with few, widely spaced bars, but varying from all scalariform to almost all simple, e.g. in *Magnolia acuminata* Linn.; the number of simple perforations varying markedly in different species, even of the same genus, being greatest in some species of *Elmerrillia* and *Magnolia*; the number of bars in the scalariform perforation plates typically fewer than 10, but, according to Garratt (746), occasionally up to 20 in *Magnolia* and up to 25 in *Talauma*. Intervascular pitting typically large and scalariform, but opposite in *Liriodendron*. Pits to ray and wood parenchyma often large and simple or with very narrow borders; often unilaterally compound, one large pit in a vessel subtending several small pits in a ray cell, the latter separated by vertical, rod-like partitions; similar to the intervascular pitting in *Liriodendron* or occasionally unilaterally compound. Tyloses often present. Mean member length 0.8–1.1 mm. **Parenchyma** in bands, 2–12 cells wide, that usually appear to be obviously 'terminal'; in some tropical species, however, there may be more than one band at the end of what appears to be a single growth ring, the inner band or bands often being discontinuous and sometimes anastomosing; Chowdhury (415) states that the position of the bands in the growth rings of *Michelia champaca* Linn. is uncertain; rare cells can occasionally be found scattered among the fibres or touching the vessels. Cells often markedly disjunctive. Silica sometimes present in *Michelia* (794). Strands usually either of 8–12 moderately short cells or of 4 tall cells. **Rays** usually up to 3 or 4 cells wide; Solereder gives a maximum of 7 for *Manglietia*; slightly less than 1 mm. high; uniseriatae usually very few, though occasionally moderately numerous, e.g. in *Magnolia pterocarpa* Roxb. and *Talauma minor* Urb., and composed of both procumbent and upright cells; 3–7 rays per mm.; heterogeneous (Kribs's Type II A and B), usually with 1–4 marginal rows of square to upright cells; homogeneous in a few species of *Magnolia*, e.g. *M. acuminata* Linn., and seldom with more than 2 marginal rows and with the cells square rather than upright in *Liriodendron*. Enlarged oil cells present on the margins of the rays in *Aromadendron*, *Elmerrillia* (Fig. 8 E), *Michelia*, and *Talauma*. Gonggrijp (794) states that silica is present in some species of *Aromadendron*, *Magnolia*, and *Michelia*. **Fibres** with small- to moderately large-bordered pits, which occur mostly on the radial walls and are typically rather few; apertures usually exserted. Occasional thin cross-walls have been noted by Janssonius (1154) near the ends of the fibres in *Magnolia javanica* Koord. et Valet. and *Michelia montana* Bl.; thin membranes (septa?) are

sometimes moderately abundant in *Manglietia glauca* Bl. and *M. hookeri* Cubitt et W. W. Sm. Walls moderately thin. Mean length 1.2–2.3 mm.

ROOT

The following characters recorded by Holm (1936) for *Liriodendron tulipifera* Linn. **Resin cells** present in the primary cortex, bark, and parenchymatous rays. Scattered sclerenchyma strands situated in the secondary **phloem**. **Pith** broad in lateral roots.

ECOLOGICAL ANATOMY

A 'dune' form of *Liriodendron tulipifera* Linn. described by Starr (2188) with smaller epidermal cells and a deeper palisade layer than in 'mesophytic' forms. Vessels more numerous in the midrib of the 'dune' form and fibres and collenchyma more abundant.

ECONOMIC USES

Numerous species and horticultural 'varieties' of *Magnolia* are cultivated for the sake of their ornamental flowers. According to Holm (1936) the bark of *Liriodendron tulipifera* Linn. was at one time used medicinally because it contains 'liriodendrin' and 'tulipiferin'.

The woods of this family are typically rather soft and easy to work and are suitable for general carpentry and joinery. That of *Liriodendron tulipifera* Linn. is of considerable commercial importance and is known under a variety of names such as Yellow Poplar (America), Whitewood (Britain), and Canary Whitewood. The timber of *Magnolia acuminata* Linn. is very similar and is also often exported from America. Various species of *Magnolia*, *Manglietia*, *Michelia*, and *Talauma* produce similar timber in the East and are of local importance, particularly *Michelia champaca* Linn., the source of Champak in India.

TAXONOMIC NOTES

The occurrence of scalariform perforation plates and scalariform intervascular pitting is generally accepted as corroborative evidence that this is a very primitive group. It should, however, be borne in mind that the vessel members are only moderately long and that the perforations appear to be in a transitional condition between wholly scalariform and wholly simple. This would indicate a moderately rather than a very low level of specialization; further, the ray type, with few uniseriats and a tendency to be homogeneous, suggests an even higher level.

In this connexion it is interesting to note that Ozenda (1645, 1647) has drawn attention to the somewhat complex nodal anatomy of *Liriodendron* and certain other members of the Magnoliaceae, and has pointed out that this is very different from the simpler node structure of the Annonaceae, Winteraceae, Dilleniaceae, and certain of the Rosaceae. The same author also found evidence of syncarpy in the Magnoliaceae. This evidence, like that of the wood anatomy, indicates that the Magnoliaceae, although a primitive group, may be less so than has sometimes been supposed.

The genera, other than *Liriodendron*, are not easily distinguished from one another by their wood anatomy. McLaughlin (1967) was unable to find any

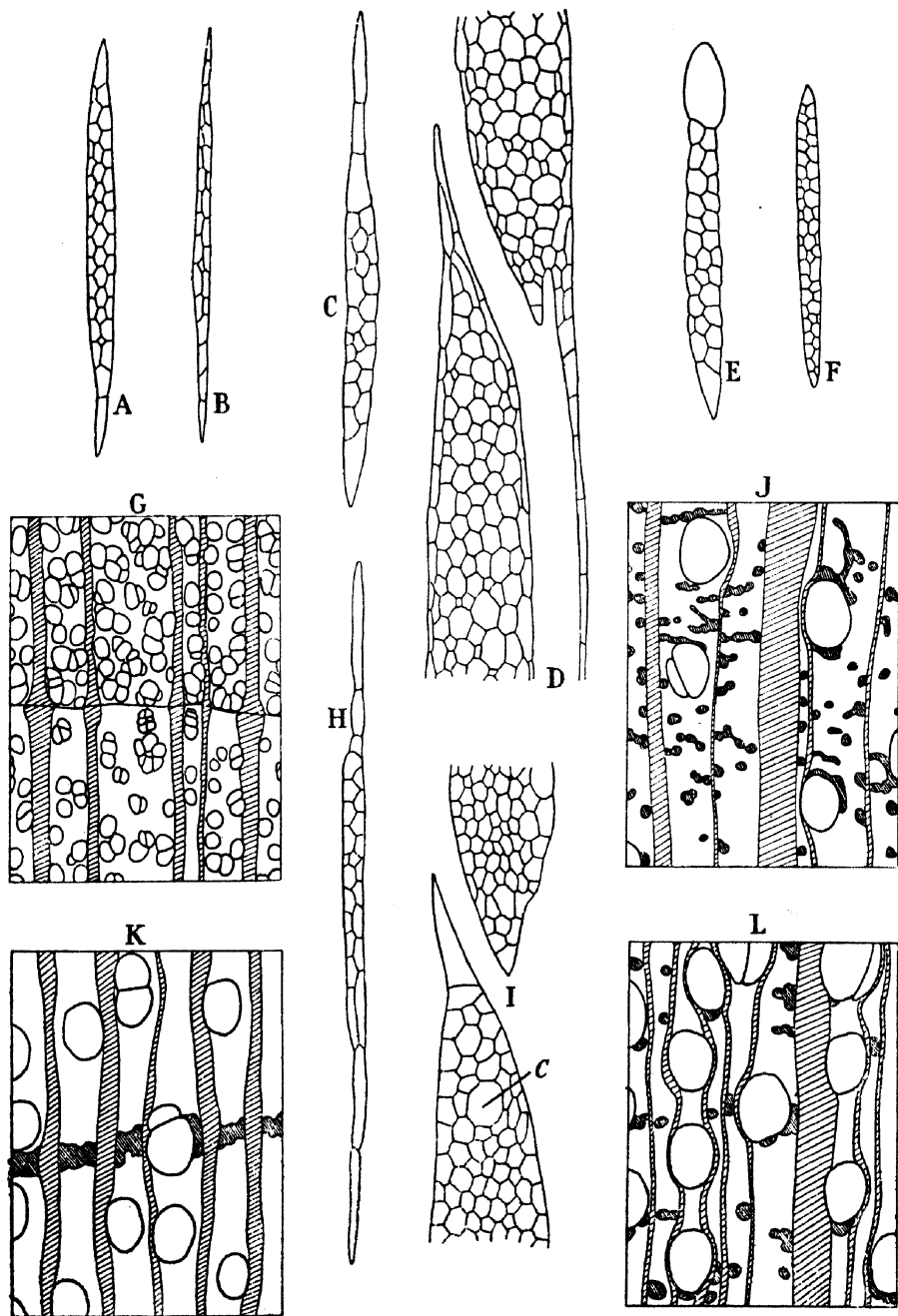


FIG. 8. **MAGNOLIACEAE**, A-B, E-G, and K; **DILLENIACEAE**, I-J and L;
SCHISANDRACEAE, C and H; **WINTERACEAE**, D

A, *Michelia champaca* Linn. Ray. B, *Manglietia virginiana* Linn. Ray. C, *Illicium cambodianus* var. *crassifolium* Ridl. Ray. D, *Drimys dipetala* F. Muell. Rays. E, *Elmerillia mollis* Dandy. Ray. F, *Liriodendron tulipifera* Linn. Ray. G, *L. tulipifera* Linn. T.S. H, *Illicium cambodianus* Ridl. Ray. I, *Dillenia reticulata* King. Rays. J, *Wormia excelsa* Jack. T.S. K, *Michelia champaca* Linn. T.S. L, *Dillenia meliosmifolia* Hook. f. et Thoms. T.S. C, cell containing raphides.

marked characteristics to distinguish *Aromadendron* and *Manglietia* from *Talauma*, or *Elmerrillia* from *Michelia*; he confirmed Dandy's statement that *Talauma spongocarpa* King is a synonym for *Michelia baillonii* F. & G. but opposed Dandy's transfer of *Michelia kachirachira* Kanehira et Yamamota and *Talauma* sp. ('Yoroconte') to *Magnolia*.

GENERA DESCRIBED

(i) GENERAL

Liriodendron,* Magnolia,* Manglietia,* Michelia,* Talauma.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Alcimandra Dandy, Aromadendron Bl., Elmerrillia Dandy, Liriodendron Linn., Magnolia Linn., Manglietia Bl., Michelia Linn., Talauma Juss.

LITERATURE

(i) On General Anatomy

Holm 1036, Lehmann 1343, Ozenda 1645, 1647, Starr 2188, Worsdell 2469.

(ii) On Wood Structure

Bailey 99, Beekman 167, den Berger 179, 182, 183, Brown, F. B. H. 280, Brown, H. P. 288, 289, Chowdhury 415, Coster 481, Desch 574, Garratt 746, 747, 747A, Gonggrijp 794, Hale 870, Howard 1088, Janssonius 1154, Jeffrey 1167, Jones 1191, Kanehira 1206, 1209, Knight 1250, Lecomte 1334, Lemesle 1351, McLaughlin 1466, 1467, Pearson and Brown 1679, Record 1790, 1818, 1843, 1851, 1883, Record and Hess 1886, Record and Mell, 1894, Stone 2203, Tang 2231, Thompson 2256, Tortorelli 2272, Tupper 2295, Yamabayashi 2478.

6. SCHISANDRACEAE

(FIG. 8 on p. 20; FIG. 9 on p. 22; FIG. 10 on p. 32)

A. AUSTROBAILEYA, KADSURA, SCHISANDRA

SUMMARY

A family of shrubs some of which have a trailing habit. Its members occur in China, the Malayan region, Australia, and in the south-eastern parts of the U.S.A., its distribution thus recalling that of the Magnoliaceae. The wood exhibits the following features. **Vessels** solitary, with spiral thickening, perforation plates scalariform or scalariform and simple, intervacular pitting scalariform to opposite, members moderately to very long. **Parenchyma** terminal only. **Rays** up to 3 cells wide, heterogeneous, with oil cells. **Fibres** with conspicuous bordered pits, of medium length to moderately long.

LEAF

Epidermis composed of mucilaginous cells in *Schisandra axillaris* Hook. f. et Thoms. and *S. elongata* Hook. f. et Thoms. Cuticle ridged, especially on the lower surface of the leaf, in *Austrobaileya scandens* Baill., and to a smaller extent in *Schisandra chinensis* (Turcz.) Baill. **Stomata** present on both surfaces in *Kadsura japonica* Juss., more numerous on the lower than on the upper surface in *Austrobaileya scandens*, confined to the lower surface in *Schisandra chinensis*; provided with specially large, oval guard cells in species

of *Austrobaileya*, *Kadsura*, and *Schisandra*. No definite subsidiary cells noted in *Austrobaileya scandens*, but a tendency to form subsidiary cells parallel to the pore observed in *Schisandra chinensis*. **Petiole**, in transverse sections through the distal end of material examined at Kew, exhibiting an arc of vascular bundles in *Kadsura japonica*; an interrupted, crescentic vascular strand in *Schisandra chinensis* (Fig. 10 J) and *S. propinqua* Hook. f. et Thoms. (Fig. 10 L); an almost continuous crescentic vascular strand in *Austrobaileya scandens* (Fig. 10 E). Ozenda (1646) found 3 vascular bundles in the base and middle part and 5 at the distal end of the petiole of *Kadsura* and *Schisandra*. The 3 strands are close together at the base of the petiole, the nodal structure being unilacunar. **Secretory elements**. Mucilage cells present around the

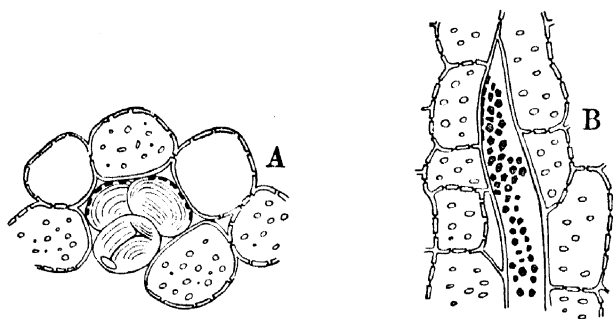


FIG. 9. SCHISANDRACEAE

Crystal-bearing fibrous cells from the pith of *Kadsura roxburghiana* Arn.: A, in transverse section; B, in longitudinal section. The crystals are shaded.—By Solereder.

petiolar vascular bundles in *Schisandra*, and mucilage cavities noted in the corresponding position in *Austrobaileya* and *Kadsura*. 'Resin' cells noted in the mesophyll and petiolar ground tissue in *Austrobaileya* and *Kadsura*.

AXIS

YOUNG STEM (Figs. 9 A-B, 10 H)

Cuticle ridged in *Austrobaileya scandens* Baill. and *Schisandra chinensis* (Turcz.) Baill. **Cork** arising superficially in material examined at Kew. **Pericycle** including a somewhat interrupted to almost continuous ring of sclerenchyma in *Schisandra*; pericyclic sclerenchyma in the form of a composite and continuous ring in *Austrobaileya scandens* and of a similar but less conspicuous and less lignified ring in *Schisandra chinensis*. **Phloem** forming an almost closed cylinder in *Schisandra*. **Xylem** appearing, in transverse sections, as an almost or quite continuous cylinder in species of *Schisandra*. A continuous ring of xylem traversed by narrow rays, also noted in *Austrobaileya* and *Kadsura*. Vessels angular in *Austrobaileya* and *Kadsura*; mostly solitary but also in tangential or oblique pairs in *Austrobaileya scandens*; mostly solitary, but tangential groups usually of more than 2 in *Schisandra chinensis*; perforation plates scalariform in both of the last 2 species (see also under 'Wood'). Lateral pits of the vessels circular with slit-shaped oblique apertures in *Austrobaileya scandens*; scalariform lateral pitting or very elongated horizontal pits noted in *Schisandra chinensis*. Groundwork of wood, in both of the same 2 species, composed of radial rows of rather thick-walled fibres, the

latter having conspicuously bordered pits with slit-shaped frequently crossed apertures. **Pith** consisting of oval, relatively thin-walled cells with granular contents in *Schisandra chinensis*; composed of fairly thick-walled, polygonal, pitted cells, in *Austrobaileya scandens*. Crystalliferous fibrous cells occur in the pith of *Kadsura roxburghiana* Arn. (Fig. 9 A-B). **Secretory elements.** Large, conspicuous, secretory cavities noted in the phloem of *Schisandra*; no secretory cavities clearly visible, though their presence suspected in the phloem of *Austrobaileya* and *Kadsura* in the material available for examination. 'Resin' cells noted in the pith of *Austrobaileya scandens*, but none seen in the corresponding position in *Schisandra chinensis*.

WOOD¹

Vessels large and solitary; 1-15 per sq. mm. in *Kadsura* and about 60 per sq. mm. in *Schisandra*; with spiral thickening. Perforation plates scalariform, with up to 15 bars in *Schisandra* and up to 7 bars in *Kadsura* (Garratt 746), and with some simple perforations and occasional reticulate plates (Lemesle 1351) in *Kadsura*. (See also under 'Young Stem'.) Intervascular pitting scalariform in *Schisandra* and typically opposite in *Kadsura*, though Lemesle (1351) refers also to scalariform pitting; pits to ray cells often unilaterally compound. Tyloses present. Mean member length in *Kadsura* 1.1 mm. (100). **Parenchyma** in terminal bands 1-3 cells wide. **Rays** 1-3 cells wide, up to 1 mm. high; heterogeneous, with uniseriate margins of 1-7 cells. Enlarged oil cells present in the marginal rows. **Fibres** with conspicuous bordered pits. Mean length 1.0-1.7 mm.

B. ILLICIUM

SUMMARY

Since it is a matter of opinion whether *Illicium* should be included in the Schisandraceae or treated as a separate family, the following brief description, which refers mainly to *Illicium verum* Hook. f., is given independently of that of the other genera included in the Schisandraceae. The wood exhibits the following features. **Vessels** solitary, perforation plates scalariform, with numerous fine bars, intervacular pitting scalariform to opposite, members very long. **Parenchyma** sparse, paratracheal, and sometimes scattered along the ring-boundary. **Rays** up to 3 cells wide, with numerous uniseriates, markedly heterogeneous. **Fibres** with conspicuous bordered pits, of medium length to moderately long.

LEAF

Glabrous. **Cuticle** on both surfaces very thick; locally striated on the upper and more universally on the lower surface. Upper **epidermis** composed of cells with sinuous anticlinal walls. **Stomata** confined to the lower surface; surrounding cells not very clearly differentiated from those of the remainder of the epidermis, but some of them containing bodies resembling plastids or secreted material. **Mesophyll** differentiated into palisade and spongy portions, but palisade consisting of 1-3 layers of almost cubical cells.

Petiole (Fig. 10 D) in transverse sections through the distal end of material

¹ Based mainly on the description given by McLaughlin (1467).

examined at Kew, exhibiting a solitary, shallow, crescentic, vascular strand. **Secretory cells** with translucent contents, readily stained with haematoxylin, abundant in the petiolar ground tissue.

AXIS

YOUNG STEM

Cuticle thick. Primary **cortex** including infrequent, unbranched, stone cells, the latter being mostly solitary but a few in small clusters. **Pericycle** with little or no sclerenchyma. **Xylem** in the form of a continuous cylinder traversed by uniseriate rays, the constituent cells of the latter filled with granular contents readily stained by haematoxylin. Vessels small, angular, mostly solitary but many in tangential or oblique pairs. Groundwork of xylem composed of radial rows of angular fibres having bordered pits with crossed apertures. **Pith**. Peripheral part consisting of cells with lignified pitted walls and wide lumina. Central pith cells thin-walled. **Secretory elements**. Abundant cells with translucent contents, readily stained with haematoxylin, present in the primary cortex, phloem, and pith.

WOOD (Fig. 8 c and H)

Vessels very to moderately small (mean tangential diameter 25–100 μ); almost exclusively solitary apart from apparent tangential pairs due to overlapping ends; 60–160 per sq. mm. Perforation plates scalariform, with very numerous (up to 150) fine bars, which often anastomose. Intervascular pitting scalariform to opposite; pits to ray cells similar. Tyloses present. Mean length about 1.3 mm. **Parenchyma** very scanty; usually paratracheal only, apart from occasional cells along the growth rings where these are distinct, and limited to a few isolated cells in contact with the vessels; McLaughlin (1467) describes the parenchyma as diffuse. Strands usually of 4–6 very tall cells. **Rays** up to 2 or 3 cells wide and up to 2 mm. high in some species; uniseriate numerous and composed of high upright cells; 10–14 per mm.; heterogeneous (Kribs's Type I), with marginal rows of very tall upright cells, usually in 2–4 rows, but 10 or more rows not uncommon. McLaughlin notes the occurrence of some rounded cells suggestive of oil cells. **Fibres** with conspicuous bordered pits on both radial and tangential walls, the apertures of the pits exserted. Kanehira (1206) refers to septate fibres in *I. anisatum* Linn. Walls moderately thick. Mean length about 1.6 mm.

TAXONOMIC NOTES (for Groups A and B)

Smith (2137) and Bailey and Nast (91) state definitely that *Illicium* should not be included in the Winteraceae, but are undecided whether it should be placed in the Schisandraceae or made the basis of a distinct family, the Illiciaceae. According to Bailey and Nast, *Illicium*, besides differing in wood structure as noted above, is also unlike the Winteraceae in the following respects. (i) The pollen is of a fundamentally different type. (ii) The primary vascular system of the stem is a continuous pseudo-siphonostele, whereas in the Winteraceae the vascular bundles form a less continuous ring. (iii) The unilacunar node structure of *Illicium* contrasts with the uniformly trilacunar nodes of the Winteraceae. (iv) The stomatal depressions of *Illicium* are not

filled with the same granular material which occurs in those of the Winteraceae. (v) There are differences in floral anatomy and morphology. (vi) There are differences in chromosome numbers. McLaughlin (1467) considers that *Kadsura* and *Schisandra* together with the Magnoliaceae *sensu stricto* form a natural group both morphologically and anatomically and that they should be retained in the Magnoliales.

The wood structure indicates that *Illicium* is distinctly the most primitive of the genera with vessels and may be regarded as intermediate in this respect between the Magnoliaceae on the one hand and *Kadsura*, *Schisandra*, and the Winteraceae on the other.

Illicium can, however, hardly be regarded as a link between these families as it differs in certain respects, e.g. in the absence of oil cells and the presence of paratracheal parenchyma, from all the other groups.

McLaughlin (1467), who refers to earlier investigations by van Tieghem and Diels respectively, confirms their suggestion that *Illicium* should be segregated from *Drimys* and its allies and made the type of a monotypic family. McLaughlin also suggests transferring this family from the Magnoliales to the Hamamelidales.

ECONOMIC USES

A fragrant oil distilled from the fruits of Star Anise (*Illicium verum* Hook. f.) is used medicinally. A chemical investigation of *I. religiosum* Siebold. has been made by Sze (2226).

GENERA DESCRIBED

GROUP A

FOR GENERAL ANATOMY. Austrobaileya,* *Kadsura*,* *Schisandra*.*

FOR WOOD STRUCTURE. *Kadsura*, *Schisandra*.

GROUP B

FOR GENERAL ANATOMY AND WOOD STRUCTURE. *Illicium*.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Bailey and Nast 91, Ozenda 1646, Rehder 1902, Smith 2137, Sze 2226.

(ii) *On Wood Structure*

Garratt 746, 747, 747A, Kanehira 1206, Lemesle 1351, McLaughlin 1467, Record 1851.

7. WINTERACEAE

(FIG. 8 on p. 20; FIG. 10 on p. 32)

SUMMARY

(i) GENERAL

A family of trees and shrubs occurring chiefly in certain parts of South-east Asia and South America. *Drimys* is the only genus which occurs in both the Old and New Worlds. Smith (2136, 2137), who has recently revised the taxonomy of the family, points out that the American species are all hermaphrodite, whereas those from the Old World are dioecious. The lower surface

of the leaf often appears punctate, owing to the **stomata** being situated in depressions filled with a white, very finely granular material, believed to be of a different chemical nature from the wax which occurs on the leaves of the Magnoliaceae. The stomata are accompanied by 2-6 cells, parallel with the guard cells. Our knowledge of the anatomy of the family has been considerably extended by the recent work of Bailey and Nast (86-91). Features in the leaf to which they draw attention include the trilacunar **nodes**; the taxonomic value of the amount of sclerenchyma around the vascular bundles of the **veins** and sheathing the terminal veinlets, increasing sclerification being interpreted as evidence of a phylogenetic advance; the occurrence of solitary and clustered, often branched, sclerenchymatous idioblasts in the mesophyll; and the presence of mesophyll cells with reticulate thickenings in certain species. The taxonomic value of the idioblasts is limited by variations in their frequency, and cannot be fully assessed without more extended examination. In young stems the **vascular bundles** are capped externally by fibres and accompanied internally by elongated, thick-walled cells, the **pericyclic fibres** becoming united by sclerosed parenchymatous cells to form a more or less continuous ring in older stems. The late secondary **phloem** includes irregular patches of sclerenchymatous tissue. Various types of scattered sclerenchymatous idioblasts and clusters of sclerosed cells are common in the cortex and pith, especially in members of the family from the Old World. **Crystals** are infrequent, but have been observed in a few species. Spherical **secretory cells** also occur.

(ii) WOOD

Vessels absent. **Parenchyma** diffuse or in fine lines and sometimes terminal. **Rays** up to 10 cells wide and very high, with numerous uniseriatae, markedly heterogeneous, occasionally with oil cells. **Tracheids** with 2-3 rows of circular pits, or occasionally with scalariform pits, on the radial walls; extremely long.

LEAF

Dorsiventral; glabrous. Lower **epidermis** papillose, e.g. in most specimens of *Drimys brasiliensis* Miers, but this character is not reliable for diagnostic purposes; papillae also variable in length. Cuticle ranging from finely alveolar to coarsely granular or warty. Epidermal cells also vary in size, form, arrangement, wall thickness, and in the nature of the pitting, but these characters are also unreliable for diagnostic purposes owing to variation within a species. **Stomata** confined to the lower surface, and restricted to depressions filled with a white granular material, the latter differing in chemical composition from the wax in the Magnoliaceae and Schisandraceae. Granular material in the stomatal depressions varying in appearance according to the drying conditions during the preparation of herbarium specimens. Stomata rubiaceous, accompanied by 2-6 cells parallel to the guard cells.

Mesophyll, in the *Wintera* section of *Drimys*, as well as in species of *Bubbia* and *Zygogynum*, including branched sclerenchymatous idioblasts, more numerous in some species than others, but frequency also varying in different collections of a single species. Mesophyll cells with reticulate thickenings noted by Bailey and Nast in *Bellium pancheri* (Baill.) v. Tiegh.

and *B. vieillardi* v. Tiegh. but not in other species of *Belliolum* examined by the same authors. Similarly thickened cells also noted in certain species of *Bubbia*.

Vascular bundles of the coarser **veins** and terminal veinlets more or less sheathed with sclerenchymatous elements in *Belliolum*, certain species of *Bubbia*, and in the *Tasmannia* section of *Drimys*. Vascular bundles of the large veins also embedded in sclerenchyma in the *Wintera* section of *Drimys*, but terminal veins in this group of species not accompanied by sclerenchyma. Considerable variation in the amount of sclerenchyma associated with the vein endings noted in *Zygogynum*. Different members of the Winteraceae form a series showing increasingly complex vascular systems in the **petiole** and lamina, the more specialized species being characterized by more numerous vascular bundles and by a tendency for the separate bundles to become fused to form an arc. Vascular system relatively simple (with an arc of vascular bundles) in *Drimys* (Fig. 10 F) and *Pseudowintera*, moderately specialized in *Belliolum* and *Bubbia* and still more advanced in *Exospermum* and *Zygogynum*. Shape and arrangement of the vascular bundles varying not only within a species but in different leaves from an individual plant. **Crystals** relatively infrequent, recorded only in *Bubbia clemensiae* A. C. Sm. and *Exospermum stipitatum* (Baill.) v. Tiegh. Spherical **secretory cells** generally present.

AXIS

YOUNG STEM

Cork arising in the epidermis in *Drimys*. Late-formed **phloem** stated by Bailey and Nast to contain irregular patches of sclerenchymatous tissue. **Xylem** of *Drimys winteri* J. R. & G. Forst. examined at Kew appearing, in transverse sections, as a more or less continuous cylinder, devoid of vessels and traversed by narrow medullary rays. Ray cells become conspicuous in sections stained with haematoxylin owing to the presence of deeply coloured contents. Bailey and Nast (88) describe the vascular bundles in the stem as being each provided with an external cap of slender, thick-walled fibres and subtended internally by elongated, lignified, thick-walled cells, the external caps of fibres becoming converted to a more or less continuous ring in older material through sclerification of the intervening parenchymatous elements. Scattered sclerenchymatous cells of varied form and clusters of sclereids observed by Bailey and Nast in the cortex and pith of some members of the family, but none seen in others. Cortex and pith of Old World representatives of the family generally more sclerified than those from the New World, especially in coriaceous species of *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum*. **Crystals** infrequent, but crystalliferous cells noted by Bailey and Nast in association with the medullary and cortical sclerenchyma in *Belliolum*, *Exospermum*, *Pseudowintera*, and *Zygogynum*. Scattered **secretory cells** noted at Kew in the phloem and in the peripheral part of the pith of *Drimys winteri*. **Nodes** trilacunar (with 3 foliar bundles related to 3 lacunae in the vascular system of the stem) in all members of the family examined by Bailey and Nast.

WOOD (Fig. 8 D)

Vessels absent. **Parenchyma** rather scanty and diffuse in *Drimys winteri* J. R. & G. Forst. and *Zygogynum* (1467), more abundant and in uniseriate

tangential lines in *Bubbia haplopus* (Burt) A. C. Smith, *Drimys colorata* Raoul, and *D. axillaris* Forst. (2256), and terminal in *Zygogynum* (1467) and the latter two species of *Drimys* (2256). Strands usually of 8–10 tall cells. **Rays** of two distinct sizes; the larger typically up to about 10 cells wide and commonly over 5 mm. high, but much wider (20 cells?) in *Pseudowintera* (88); uniseriates numerous, often more than 1 mm. high and composed of tall upright cells; 9–13 rays per mm.; markedly heterogeneous (Kribs's Type I) with up to 10 or more marginal rows of tall upright cells; the inner cells sometimes square rather than procumbent in *Drimys*, but procumbent in *Bubbia haplopus*; often with sheath cells. Oil cells reported in the rays of *Zygogynum* (1467). **Tracheids** usually with large, circular, bordered pits in the radial walls, the pits most commonly in two or three rows and with included apertures; the pits tend to be elongated or even scalariform in the early wood tracheids in some species of *Drimys* and *Bubbia*, particularly in the overlapping end-walls, the ratio of round to scalariform pits varying even from specimen to specimen (88). Pits to ray cells similar to the pits to other tracheids. Mean length (*Bubbia* and *Drimys*) 4.0–4.3 mm. and, according to McLaughlin (1467) up to 5.1 and 6.3 mm. respectively in *Drimys* and *Zygogynum*.

TAXONOMIC NOTES

(i) BASED ON WOOD STRUCTURE

Bailey and Nast (88, 91), in their study of the morphology of this group, have shown that, with the exclusion of *Illicium*, 'the Winteraceae become a homogeneous, natural aggregation of obviously closely related plants'. Within the group these authors distinguish the following trends of structural specialization: 'toward reduction or elimination of wood parenchyma in Sect. *Wintera* of *Drimys*, toward excessively widened multiseriate rays in *Pseudowintera*, and toward reduction of cell size, particularly in dwarfed or microphyllous species, e.g. in Sect. *Tasmannia* of *Drimys*'.

The occasional scalariform pitting that occurs in the tracheids of *Drimys* figured largely in the controversy of about 1918, associated with the names of Bailey and Jeffrey, as to whether *Drimys*, *Tetracentron*, and *Trochodendron* represent degenerate 'evascularized' Dicotyledons, whose ancestors possessed true vessels in their secondary xylem, or whether they have descended directly from ancestors that possessed scalariform tracheids in their secondary xylem (99, 1167, 2256). Modern work on the significance of the length of the cambial initial and vessel members (see Introduction) has provided a means of testing such hypotheses and Bailey and Nast, writing in 1945, state that 'the primitive character of the cambium and xylem in the Winteraceae, *Trochodendron* and *Tetracentron* rules out any possibility of these plants having developed vessels and subsequently having lost them'. Elsewhere they claim that 'when the summation of evidence from all organs and parts of the plants is taken into consideration, there are no convincing arguments for deriving the Trochodendraceae from the Winteraceae or vice versa, or even for inferring that these families are closely related genetically. Nor can one assume that the other ranalian families were derived from these vesselless families.'

The same authors also point out that comparisons between the Winteraceae

and the Coniferae overlook important anatomical differences, such as occur in the rays, and are thus misleading. They conclude that 'if the vesselless wood of the Winteraceae is to be compared with that of the Gymnosperms, it should be with the secondary xylem of Pteridospermae and Bennettitales rather than with that of the Coniferae, Ginkgoales or Cordaitales'.

(ii) BASED ON GENERAL ANATOMY

Besides the evidence of wood structure, Bailey and Nast (91) consider that other anatomical facts indicate that *Illicium* should not be included in the Winteraceae, a view which is also supported by Smith (2137) on morphological grounds. This subject is discussed more fully under Schisandraceae. Bailey and Nast (1944) also say that:

'The available evidence indicates that internal foliar characters are unstable and variable in the Winteraceae, particularly in *Bellium*, *Bubbia* and *Zygogynum*. . . . In the *Wintera* section of *Drimys*, increasing coriaceousness is attained largely by the formation of large, armed sclereids interspersed throughout the mesophyll. On the contrary, in the *Tasmannia* section of *Drimys*, sclerification progresses along the veins and veinlets, the bulk of the mesophyll remaining thin-walled. In *Bellium*, *Bubbia* and *Zygogynum*, increasing coriaceousness commonly involves intensified sclerification along the veins and veinlets, and not infrequently throughout the mesophyll. In the more coriaceous species of *Bubbia* and *Zygogynum*, all three trends of sclerification may occur simultaneously.'

ECONOMIC USES

Winter's Bark (*Drimys winteri* J. R. & G. Forst.) has been valued for its antiscorbutic properties, but is not now of much importance. True Winter's Bark has frequently been confused with that of other plants. The following microscopical characters were noted in specimens in the Kew Museums. Exterior of the young bark covered by about 4 or 5 layers of very thick-walled cork cells, the thickening being uniform on all of the walls, and the lumen filled with gum-like deposits. Cork plentiful in old material, but very uneven and giving the exterior of the bark a very rough appearance. Cork bounded internally by a parenchymatous cortex, the inner boundary of this region being marked by groups of very large, thick-walled stone cells, the latter sometimes associated with groups of fibres very much smaller in diameter but also thick-walled. These parenchymatous elements collectively form a very much interrupted ring. Smaller, isolated stone cells also present immediately within the cork layer. Solitary, vertically elongated, secretory cells with pale-yellow contents abundant in the phloem on the inside of the sclerenchyma ring. Phloem in old bark very much broader and containing radially arranged groups of stone cells. More numerous secretory cells also occur throughout the phloem. Unlignified phloem elements of the older bark tend to be in radial rows.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Bellium, *Bubbia*, *Drimys*,* *Exospermum*, *Pseudowintera*, *Zygogynum*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Bubbia, *Drimys*, *Zygogynum*.

LITERATURE

(i) *On General Anatomy*

Bailey 75, Bailey and Nast 86, 87, 88, 89, 90, 91, 92, Jeffrey and Cole 1167, Knight 1250, Nast 1580, Smith, A. C. 2136, 2137, 2139.

(ii) *On Wood Structure*

Bailey and Nast 88, 91, 94, Cozzo 494, Dadswell and Record 533, Hess 950, McLaughlin 1467, Thompson 2256.

8. CERCIDIPHYLLACEAE

(FIG. 7 on p. 14; FIG. 10 on p. 32)

SUMMARY

(i) GENERAL

Trees from China and Japan, with leaves somewhat similar to those of the Hamamelidaceae. The sole genus is *Cercidiphyllum* of which *C. japonicum* Sieb. et Zucc. has been examined.

(ii) WOOD

Vessels very small and numerous, with spirals in the tips of members, perforation plates scalariform with numerous bars, intervacular pitting scalariform to opposite, members very long. **Parenchyma** very sparse, terminal and sometimes diffuse. **Rays** 1-2 cells wide, heterogeneous, and often fused vertically. **Fibres** with conspicuous bordered pits, moderately long.

LEAF

Dorsiventral. Lower **epidermis** sub-papillose. Leaf margins provided with **glandular emergences** containing a gummy substance. **Stomata** confined to the lower surface; ranunculaceous. **Petiole** (Fig. 10 N) in transverse sections through the distal end, exhibiting a solitary, U-shaped vascular strand with very much incurved ends. Petiolar vascular strand accompanied on the outside by an interrupted ring of fibres. Large cluster **crystals** present in the mesophyll as well as in the cortical region of the petiole.

AXIS

YOUNG STEM (Fig. 10 M)

Cork originating in the outer part of the cortex. **Pericycle** including isolated bundles of fibres. A slightly interrupted ring of similar fibres also arising in the **phloem**. **Xylem** in the form of a continuous cylinder traversed by narrow rays; including numerous vessels, very angular in transverse section and tending to exhibit a radial arrangement, but tangential or oblique pairs as well as small clusters also common. Individual vessel-elements, where adjacent, separated from one another by very thin walls. Perforation plates scalariform with numerous, very fine bars. **Pith** composed of thick-walled cells, mostly filled with starch. Perimedullary cells smaller than those constituting the greater part of the pith. Large cluster **crystals** present in the young primary cortex but tending to disappear from older material. Many of the medullary ray cells, where traversing the phloem, contain large, conspicuous, solitary crystals.

WOOD (Fig. 7 I-J)

Vessels very small (mean tangential diameter 25-50 μ) and angular; solitary and in short radial multiples and tangential pairs due to overlapping ends (Fig. 7 I); more than 100 per sq. mm. and crowded; coarse spirals present in the vessel tips. Perforation plates scalariform, with 20-50 bars (1467). Intervascular pitting very scarce; when present, opposite to scalariform; pits to ray cells similar to the intervascular pitting, often unilaterally compound. Tyloses sometimes present. Mean member length 1.6 mm. (100). **Parenchyma** sparse and limited to the boundaries of the growth rings in the material examined, but McLaughlin (1467) refers to diffuse parenchyma, the terminal parenchyma varying from occasional cells to discontinuous uniseriate bands. **Rays** up to 2 cells wide and less than 1 mm. high; often with 2 or more multiseriate parts separated by uniseriate upright cells and with the latter nearly as wide tangentially as the multiseriate parts (Fig. 7 J); uniseriates moderately numerous and composed of both procumbent and upright cells; about 13 rays per mm.; heterogeneous (Kribs's Type II B), with 1-4 marginal rows of square to upright cells. Cells often containing brown deposits and sometimes crystals of calcium oxalate (1467). **Fibres** with conspicuous bordered pits, which are equally numerous on both radial and tangential walls and of about the same size as the opposite intervascular pitting. Walls of medium thickness and usually markedly flattened in the last 2-8 rows, forming a distinct band of latewood from which vessels tend to be absent. Mean length 1.9 mm. (100).

TAXONOMIC NOTES

McLaughlin (1467) considers that this family is more closely allied to the Hamamelidales than to the Magnoliales.

GENUS DESCRIBED

Cercidiphyllum.*

* Represented in the Kew slide collection.

LITERATURE

On Wood Structure

Bailey and Tupper 100, Kanehira 1206, 1209, McLaughlin 1466, 1467, Record 1843, 1851.

9. EUCOMMACEAE

(FIG. 7 on p. 14; FIG. 10 on p. 32)

SUMMARY

(i) GENERAL

The family is represented by a single Chinese tree *Eucommia ulmoides* Oliv. The most noteworthy anatomical feature is the occurrence of **laticiferous cells** containing a substance similar to rubber. This material is liberated from the bark, young twigs, and leaves when broken or removed from the plant. The laticiferous elements occur particularly in the phloem and adjacent tissue of the pericycle, although they extend into the mesophyll of the leaf.

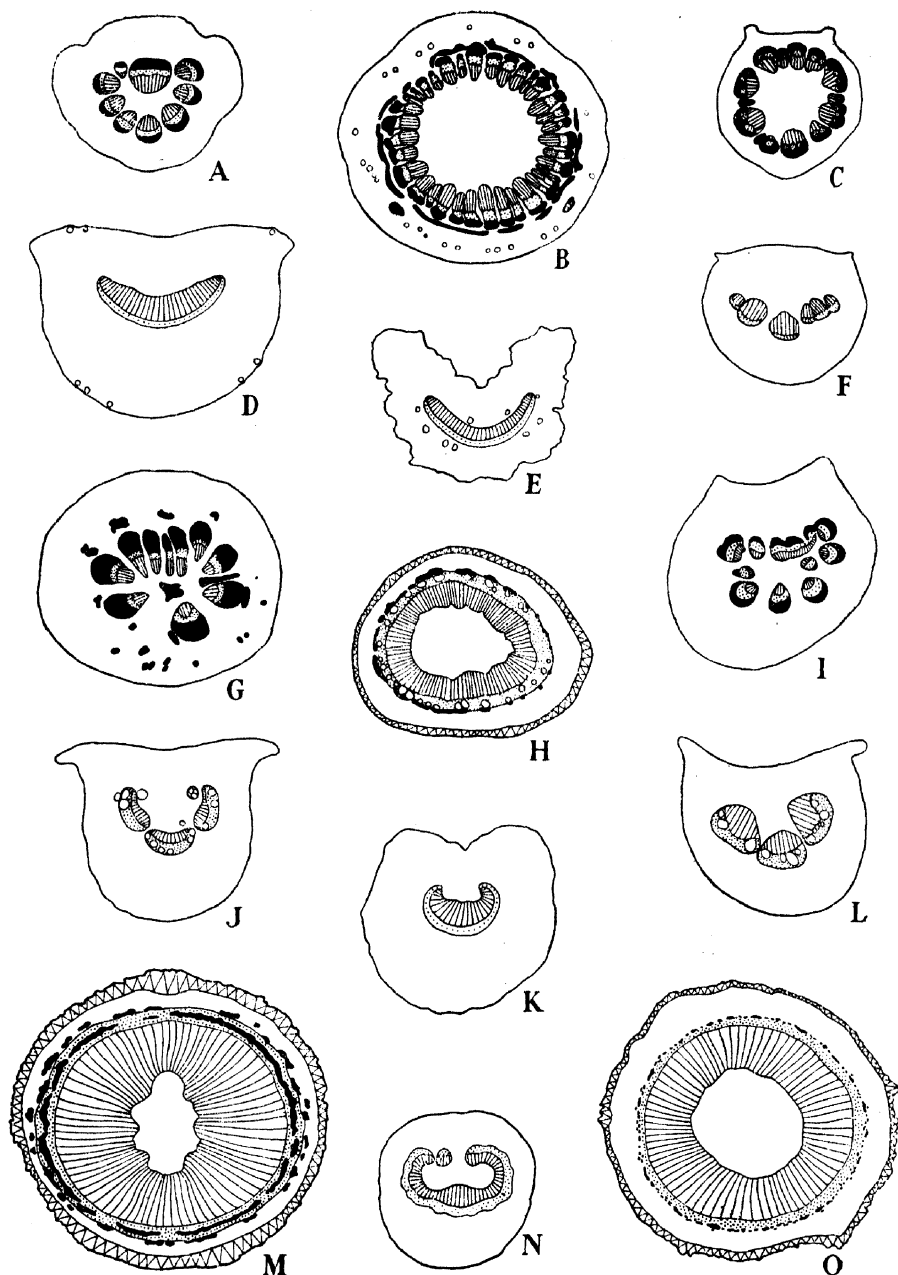


FIG. 10. **MAGNOLIACEAE**, A-C, G, and I; **SCHISANDRACEAE**, D-E, H, J, and L; **WINTERACEAE**, F; **EUCOMMIACEAE**, K and O; **CERCIDIPHYLLACEAE**, M-N
A, *Magnolia virginiana* Linn. Petiole $\times 19$. B, *M. grandiflora* Linn. Stem $\times 10$ (secretory cavities in cortex). C, *Liriodendron tulipifera* Linn. Petiole $\times 10$. D, *Illicium verum* Hook. f. Petiole $\times 13$ (secretory cavities in ground tissue). E, *Austrobaileya scandens* Bail. Petiole $\times 13$. F, *Drimys winteri* Forst. Petiole $\times 10$. G, *Magnolia grandiflora* Linn. Petiole $\times 10$. H, *Schisandra propinqua* Hook. f. et Thoms. Stem $\times 20$. I, *Michelia excelsa* Blume. Petiole $\times 13$. J, *Schisandra chinensis* (Turcz.) Baill. Petiole $\times 13$. K, *Eucommia ulmoides* Oliver. Petiole $\times 19$. L, *Schisandra propinqua* Hook. f. et Thoms. Petiole $\times 20$. M, *Cercidiphyllum japonicum* Sieb. et Zucc. Stem $\times 19$. N, *C. japonicum* Sieb. et Zucc. Petiole $\times 29$. O, *Eucommia ulmoides* Oliver. Stem $\times 19$.

According to Varossieau (2325) the laticiferous tubes are unicellular (inarticulate), and differ in their mode of development from those of *Cannabis* and *Euphorbia*.

(ii) WOOD

Vessels very small and nearly all solitary, semi-ring-porous, with spiral thickening, perforations simple, intervascular pitting opposite to alternate, members of medium length. **Parenchyma** diffuse and terminal. **Rays** up to 3-4 cells wide and low, with rather few uniseriades, almost homogeneous. **Fibres** with distinctly bordered pits, moderately to very short.

LEAF

Dorsiventral. **Hairs** simple, unicellular. **Mesophyll** including groups of silicified cells. **Stomata** confined to the lower surface; ranunculaceous. **Petiole** (Fig. 10 K), in transverse sections through the distal end, exhibiting single, thick, crescent-shaped vascular strand, including xylem vessels arranged in radial rows. **Laticiferous cells** mostly situated in the veins, but sometimes in the mesophyll as well. **Crystals** absent.

AXIS

YOUNG STEM (Fig. 10 O)

Cork originating in the epidermis. Primary **cortex** collenchymatous. **Pericycle** containing a loose ring of fibres, together with elongated stone cells with silicious contents and thin-walled, frequently paired, parenchymatous cells each containing an areolate silica body. **Xylem** and **phloem** in the form of continuous cylinders traversed by narrow rays. **Pith** heterogeneous, the walls of the peripheral cells being thicker than those of the cells towards the centre. **Laticiferous cells** occur in the primary cortex, phloem, and pith.

WOOD (Fig. 7 K-L)

Vessels very to extremely small (mean tangential diameter usually about 25-30 μ); nearly all solitary, but with occasional radial pairs; 250-350 per sq. mm. (2262); semi-ring-porous; with spiral thickening. Perforations simple, except in the immediate neighbourhood of the primary xylem (2158). Interspiracular pitting uncommon owing to the solitariness of the vessels; small, opposite (2261) to alternate; pits to ray and wood parenchyma cells similar in size and shape to the interspiracular pits. Tyloses reported (2262) in a single specimen. Mean length 0.36-0.5 mm. (2262). **Parenchyma** apotracheal, as isolated cells scattered among the fibres (Fig. 7 L) and along the boundaries of the rings. Strands usually of 4 cells. **Rays** up to 3, occasionally 4, cells wide and seldom more than 0.5 mm. high; uniseriades rather few and composed mostly of procumbent cells; about 5 rays per mm.; almost homogeneous (intermediate between Kribs's Types Heterogeneous II B and Homogeneous I), with an occasional single marginal row of square to slightly upright cells; the procumbent cells small (Fig. 7 K). **Fibres** with distinctly bordered pits on both radial and tangential walls, the borders slightly smaller than those of the interspiracular pits. Walls moderately to very thick. A few cells with spiral thickening present in some specimens. Mean length 0.67-0.84 mm. (2262).

ROOT

Laticiferous cells present in the pericycle and phloem.

TAXONOMIC NOTES

Tippo (2261, 2262) places the Eucommiaceae in the Urticales near the Ulmaceae and at about the same level of specialization. A similar position is suggested by Varossieau (2324) on general morphological grounds. Among the characters of the wood that Tippo considers as evidence of similarity with Ulmaceae rather than Hamamelidaceae are simple perforation plates, ring-porous vessels, ray type, and alternate intervacular pitting.

ECONOMIC USES

The bark of *E. ulmoides* has been used for medicinal purposes by the Chinese. The rubber has never been extracted commercially owing to the small quantity present in the latex.

GENUS DESCRIBED

Eucommia.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Harms 898, Parkin 1654, Varossieau 2324, 2325.

(ii) *On Wood Structure*

Record 1843, 1851, Tippo 2261, 2262, Varossieau 2324.

10. EUPTELEACEAE

(FIG. 11 on p. 40)

SUMMARY

Following the taxonomic revision by Smith (2140), the Eupteleaceae are here treated as a unigeneric family comprising 2 species of trees. These are *E. polyandra* Sieb. et Zucc. from Japan and *E. pleiosperma* Hook. f. et Thoms. from China and parts of India. Smith was unable to recognize *E. francheti* v. Tiegh. as a separate species, since it cannot reliably be separated from *E. pleiosperma* by having a less papillose lower epidermis to the leaf than the last species. The **wood** exhibits the following features. **Vessels** small, solitary, numerous, and with scalariform perforation plates; intervacular pitting mostly opposite, members of medium length to moderately long. **Parenchyma** in narrow terminal bands. **Rays** up to 10 cells wide and high, heterogeneous. **Fibres** with small bordered pits, of medium length.

LEAF

Dorsiventral. **Hairs** on young leaves simple, uniseriate, with a single or several short basal cells, sometimes arranged bi-serially, together with one or more elongated terminal cells with wide lumina. Lower **epidermis** frequently papillose in *E. pleiosperma* Hook. f. et Thoms. **Stomata** on the lower surface ranunculaceous and less specialized than in *Tetracentron* and *Trochodendron*. Arm-palisade cells recorded in the **mesophyll**. **Petiole** of *E. pleiosperma* (Fig. 11 G) in transverse sections through the distal end of

material cultivated and examined at Kew, exhibiting a cylindrical vascular strand, tending to become double with two groups of xylem on the adaxial side and supported along the whole of the outer periphery by a well-developed ring of fibres. One or two small accessory strands also present on the adaxial side. Vessels in the xylem arranged in very definite radial rows. The following additional particulars concerning the petiole structure have been recorded by Nast and Bailey (93). Five-11 vascular strands (more numerous in *E. pleiosperma* than in *E. polyandra*) enter the base of the petiole and, at certain levels of the attachment of the leaf, commingle with those of the axillary bud to form an arc of vascular strands confronting a single broad parenchymatous region of the eustele. Vascular bundles first uniting nearer the distal end of the petiole to form a more or less continuous arc, and, still closer to the lamina, a vascular cylinder which extends into the midrib. No branched idioblasts, either sclerotic or secretory, noted by Nast and Bailey, but **secretory cells** with unidentified contents observed at Kew in the 'cortical' and 'medullary' ground tissue of the petiole of *E. pleiosperma*, and smaller, apparently tanniferous elements in the phloem and medullary ray cells in the petiole of the same species. A few cluster **crystals** noted in the parenchymatous ground tissue of the petiole of *E. pleiosperma*.

AXIS

YOUNG STEM (Fig. 111)

The following description applies mainly to *E. pleiosperma*. **Cork** arising at a fairly deep level in the cortex. **Pericycle** including a continuous or slightly interrupted sclerenchymatous ring, the latter consisting mostly of fibres but with a small number of stone cells present as well. **Phloem** containing no parenchymatous elements in the material examined. **Xylem** containing very numerous, somewhat angular vessels, seldom more than $30\ \mu$ in diameter. Vessels tending to be in radial rows in the first-formed wood, but this character less marked in the later wood where they are solitary or in variously arranged groups; perforation plates scalariform with numerous fine bars. Primary rays 1-3 cells wide, conspicuous; distal ends enlarged. **Pith** consisting of relatively thick-walled cells filled with starch. Large, conspicuous, cluster **crystals** present in the cortex, especially in the inner part. **Secretory cells** with unidentified contents also noted in the cortex.

WOOD

Vessels small (mean tangential diameter about $50\ \mu$) and solitary; about 75 per sq. mm. in the material examined, but McLaughlin (1467) gives the number as 120-250 per sq. mm. Perforation plates scalariform, with 20-90 bars. Intervascular pitting opposite to transitional, rarely alternate or scalariform; pits to ray cells unilaterally compound. With thin-walled tyloses. Mean member length 0.8-0.9 mm. **Parenchyma** in terminal bands 1-2 cells wide. **Rays** up to 10 cells wide and 3 mm. high; uniseriate numerous, composed mainly of upright cells, but occasionally with some square to slightly procumbent cells; about 9 rays per mm.; heterogeneous, with 1-6 marginal rows of square or upright cells (Kribs's Type II A) on the outside of mature stems, more markedly heterogeneous (Type I) in small twigs (93). **Fibres** with small, round, bordered pits, the apertures exserted; mean length 1.2-1.5 mm.

TAXONOMIC NOTES

Although *Euptelea* has commonly been treated as a representative of the Trochodendraceae, the recent researches of Smith (2140) and of Nast and Bailey failed to reveal any important similarities between *Euptelea* and the other two genera. The wood structure in particular is completely unlike that of the Trochodendraceae. All three authors agree that *Euptelea* occupies a rather isolated taxonomic position, although its affinities are regarded as rather remotely ranalian.

GENUS DESCRIBED

Euptelea.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Nast and Bailey 93, Smith 2140.

(ii) *On Wood Structure*

Bailey and Nast 93, Kanehira 1206, McLaughlin 1466, 1467, Record 1851.

11. HIMANTANDRACEAE

(FIG. 7 on p. 14; FIG. 11 on p. 40)

SUMMARY

According to Bailey, Nast, and Smith (94) the family consists of 2 principal species of trees, i.e. *H. belgraveana* F. v. Muell. from New Guinea and probably the North Moluccas and *H. baccata* (F. M. Bailey) Diels from Queensland. There is a third inadequately known species *H. parviflora* (Bak. f.) Norm. in New Guinea. The lower surface of the leaves bears an indumentum of **peltate scales**. The wood exhibits the following features. **Vessels** with faint spiral thickening, simple perforations, intervacular pitting alternate, members moderately long. **Parenchyma** in concentric bands. **Rays** mostly 2-3 cells wide, heterogeneous, and with intercellular spaces. **Fibres** with bordered pits, of medium length to moderately long.

LEAF

Abaxial surface covered with a dense indumentum of **peltate scales**, those of *H. baccata* smaller and less crowded than those of *H. belgraveana*. Upper surface of mature leaves glabrous, but scales or stellate hairs noted by Bailey, Nast, and Smith on the adaxial surface of immature leaves of certain specimens. **Stomata** characteristically arranged in approximately circular clusters around each of the peltate scales on the lower surface. **Mesophyll** said by the same authors to include numerous, scattered clusters of sclereids, in all of the specimens of *H. belgraveana* collected by Clemens, but sclereids infrequent in or absent from other material which they examined. **Petiole** of *H. belgraveana* (Fig. 11 H), in transverse sections through the distal end of specimens examined at Kew, exhibiting an outer cortical region composed of thick-walled cells; inner cortical and medullary regions composed of cells with much thinner walls apart from scattered groups of large, pitted, lignified

stone cells; a vascular system consisting of a circle of separate, collateral bundles, each supported externally by groups of fibres. Petiole described by Bailey, Nast, and Smith as having 3 vascular strands entering the base, the traces dividing towards the distal end to form 6–8 bundles arranged so as to appear as an interrupted circle when viewed in transverse sections. Pairs or small clusters of **crystals** present in the cells of the lower epidermis, and in strands accompanying the sheaths of sclerenchyma enclosing the vascular bundles of the veins and veinlets. Spherical **secretory cells** abundant.

AXIS

YOUNG STEM (Fig. 11 J)

The following description is based on an examination of *H. belgraveana* grown at Kew, and on the notes recorded by Diels (583), and the account published by Bailey, Nast, and Smith (94).

Cork arising in the sub-epidermis when still very young; component cells very strongly thickened on the inner tangential, and to a smaller extent on the lateral walls. Primary **cortex** containing groups of very thick-walled cells which become attached locally to the outer part of the pericyclic sclerenchyma. **Pericycle** with a composite, somewhat interrupted ring of sclerenchyma. **Phloem** narrow, devoid of lignified elements in the young material examined at Kew, but phloem of older stems described by Bailey, Nast, and Smith (94) as stratified into fibrous and non-fibrous portions. Sieve tubes similar to those of the Magnoliaceae. Primary vascular system appearing in transverse sections as a circle of individually distinct **vascular bundles**, but this character becomes less obvious with the onset of secondary thickening, many of the rays being only 1 cell wide. **Xylem** including numerous vessels up to about 45 μ in diameter, tending to be in radial rows, with bordered pits on the lateral walls and mixed scalariform perforation plates and simple perforations; fibres with bordered pits; rays mostly 1–2 cells wide. Bailey, Nast, and Smith record the occurrence of a higher proportion of scalariform perforation plates and more frequent opposite pitting in the lateral walls of vessels from the metaxylem and first-formed secondary xylem than in the later secondary xylem. (See 'Wood' below.) **Nodes** trilacunar according to Bailey, Nast, and Smith. **Pith** broad, consisting of pitted cells, but also including groups of stone cells which tend to form transverse diaphragms. Isolated **secretory cells** with unidentified amorphous contents noted in the primary cortex. Solitary **crystals** present in many of the cortical stone cells, and, according to Bailey, Nast, and Smith, in parenchymatous cells adjacent to the phloem fibres.

WOOD¹ (Fig. 7 G–H)

Vessels medium-sized (100–200 μ mean tangential diameter); solitary, in multiples of up to 4 cells and in irregular groups; McLaughlin notes very indistinct spiral thickening. Perforations typically simple, but Record (1851) lists this family as having both scalariform and simple perforation plates. (See also under 'Young Stem'.) Intervascular pitting alternate, of medium size; pits to ray and wood parenchyma similar. Members up to 1 mm. long. **Parenchyma** in continuous bands 2–20, mostly 3–8, cells wide, and about

¹ Based mainly on the description given by R. P. McLaughlin (1467).

half a millimetre apart (Fig. 7 H). Strands usually of 8 cells. **Rays** up to 4, mostly 2-3, cells wide, slightly more than 1 mm. high and heterogeneous, with 2 or 3 (occasionally 4) marginal rows of upright cells. Intercellular spaces moderately conspicuous. **Fibres** with bordered pits, which occur mostly on the radial walls, with exserted apertures. Walls of medium thickness. Up to 2 mm. long.

TAXONOMIC NOTES

Himantandra is treated in the Engler system as well as in that of Hutchinson (1113) as a separate family related to the Magnoliaceae. This treatment is fully supported by the more recent work of Bailey, Nast, and Smith. The presence in *Himantandra* of secretory cells, of sclerenchymatous diaphragms in the pith, the occurrence of vessels with simple perforations and scalariform perforation plates and the ring of separate bundles in the petiole are all characters which suggest affinities with the Magnoliaceae. Peltate scales of the kind which occur in *Himantandra* have not been recorded in the Magnoliaceae and other families which are usually regarded as being closely related. It is interesting to note that stellate hairs and scales occur in certain species of *Hibbertia* (Dilleniaceae) which Hutchinson (1113) regards as derived from the Magnoliales. From a study of the wood, McLaughlin (1467) concludes that *Himantandra* would be more appropriately placed with the Annonales than the Magnoliales.

GENUS DESCRIBED

Himantandra.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Bailey, Nast, and Smith 94, Diels 583, Hutchinson 1113.

(ii) *On Wood Structure*

McLaughlin 1467, Record 1843, 1851.

12. LACTORIDACEAE

SUMMARY

A small family consisting of the single shrub *Lactoris fernandeziana* Phil. from Juan Fernandez. The wood exhibits the following features. **Vessels** small, perforations simple, intervacular pitting alternate, members very short. **Parenchyma** diffuse. **Rays** very broad and high, composed of upright cells. **Fibres** with small bordered pits, extremely short.

LEAF

Cells of the lower **epidermis** described by Solereder as papillose. **Secretory cells** present in the spongy mesophyll.

AXIS

STEM

Pericycle including crescent-shaped strands of fibres. **Vascular bundles** separated from one another by medullary rays 2-3 cells wide. **Tannin sacs**, frequently arranged in longitudinal rows, present in the pith.

WOOD¹

Vessels small (less than 100 μ mean tangential diameter); solitary and in radial multiples; up to 18 per sq. mm. Perforations simple. Intervascular pitting alternate and small. Members less than 0.3 mm. **Parenchyma** apotracheal, diffuse. **Rays** extremely high and as broad as the intervening areas of fibres; composed entirely of upright cells. **Fibres** with numerous, small, irregularly distributed, bordered pits; up to 0.5 mm. long.

TAXONOMIC NOTES

The genus *Lactoris* was included in the Piperaceae in the Bentham and Hooker system, but it is now generally regarded as having affinities with the Magnoliaceae. McLaughlin, however, in a study of the wood anatomy of the Magnoliales in 1933, came to the conclusion that the Lactoridaceae should be transferred to the Piperales.

GENUS DESCRIBED

Lactoris.

LITERATURE

On Wood Structure

McLaughlin 1937, Record and Hess 1886.

13. TROCHODENDRACEAE

(FIG. 7 on p. 14; FIG. 11 on p. 40)

SUMMARY

The family is here treated as unigeneric, and comprising the single genus *Trochodendron* as proposed by Smith (2139), the sole representative being *T. aralioides* Sieb. et Zucc., a tree which occurs in Japan and Formosa, and is cultivated elsewhere. One of the most striking anatomical features is the diverse forms of sclerenchymatous idioblasts which occur in the leaf and in the inner part of the primary cortex of the stem. The wood exhibits the following characters. **Vessels** absent. The greater part of the tissue formed of extremely long **tracheids** with circular to scalariform pits on the radial walls. **Parenchyma** diffuse. **Rays** of 2 sizes, the larger up to 12 cells wide; markedly heterogeneous.

LEAF

Dorsiventral. Upper **epidermis** composed of cells with very thick outer walls. **Stomata** (Fig. 11 F) confined to the lower surface, subtended by cuticular vestibules, and each accompanied by 2 horseshoe-shaped subsidiary cells, the latter forming a circle around each of the stomata. Subsidiary cells, at least in living specimens, also clearly demarcated from the remainder of the epidermis by the presence of deposits of a gum-like substance secreted in

¹ Based on the descriptions by McLaughlin (1937) and Record and Hess (1886).

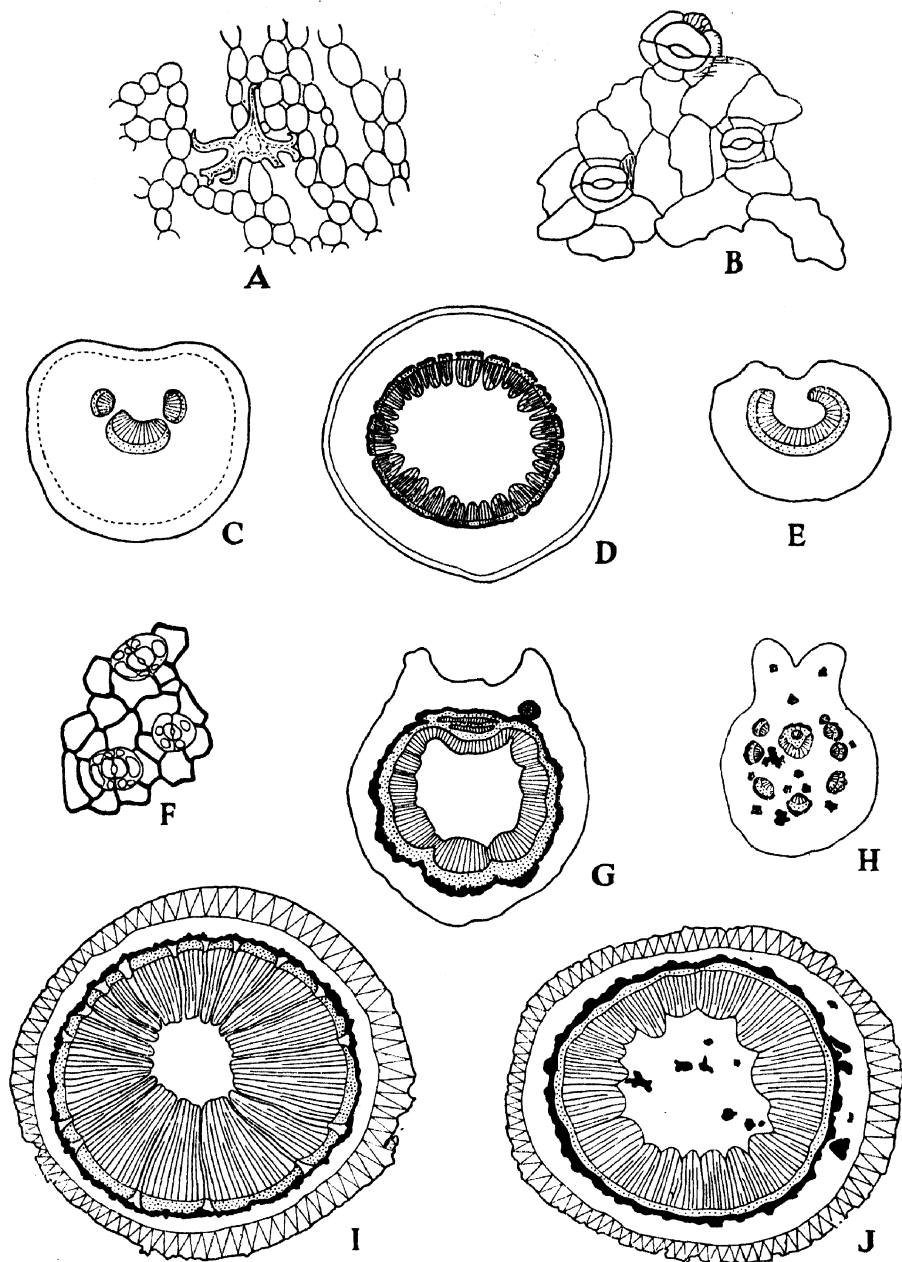


FIG. 11. *TROCHODENDRACEAE*, A, C-D, and F; *TETRACENTRACEAE*, B and E; *EUPTELEACEAE*, G and I; *HIMANTANDRACEAE*, H and J

A, *Trochodendron aralioides* S. et Z. Cortical tissue showing lacunae and sclereids $\times 100$. B, *Tetracentron sinensis* Oliv. Stomata from lower epidermis of leaf $\times 167$. C, *Trochodendron aralioides* S. et Z. Petiole $\times 13$. D, *T. aralioides* S. et Z. Stem $\times 8$. E, *Tetracentron sinensis* Oliv. Petiole $\times 13$. F, *Trochodendron aralioides* S. et Z. Stomata from lower surface of leaf $\times 167$. G, *Euptelea pleiosperma* Hook. f. et Thoms. Petiole $\times 28$. H, *Himantandra belgraveana* Diels. Petiole $\times 19$. I, *Euptelea pleiosperma* Hook. f. et Thoms. Stem $\times 19$. J, *Himantandra belgraveana* Diels. Stem $\times 12$.

In Figs. C and D well-developed intercellular spaces and numerous sclerenchymatous idioblasts occur in the inner but not in the outer part of the cortex.

the cells. **Mesophyll** consisting of 2, or locally of 3, layers of palisade tissue and very lacunar spongy tissue. Intercellular spaces of the spongy tissue occupied by very large, branched, sclerenchymatous idioblasts (Fig. 11 A). Vascular bundles of the **veins** embedded in the mesophyll, the larger ones accompanied by fibres. Inner cortical region of the **petiole** (Fig. 11 C) very lacunar, with idioblasts, somewhat resembling those of the lamina, in the intercellular spaces.

Idioblasts in the inner lacunar tissue of the petiole, described by Foster (695, 696) as occasionally in longitudinal series of 3 connected cells, but more usually isolated by parenchymatous elements. The laminar idioblasts, according to the same author, vary from 'radiately branched elements with dichotomous arms to bizarre asymmetrical, cruciform and fibre-like forms'. Idioblasts vary in frequency in different specimens; small clusters of irregular thick-walled types noted by Foster in certain material from Formosa 'above the juncture of the veins supplying each marginal tooth'. Vascular system of the petiole appearing, in transverse sections through the distal end of material grown at Kew, as a solitary, slightly interrupted, arc-shaped strand, mostly composed of xylem consisting of radial rows of tracheids.

According to Bailey and Nast (92), in large leaves 5-7 vascular strands enter the base of the petiole, coalescing at a higher level to form an arc, sometimes accompanied by 2 adaxial bundles, this structure extending upwards through the petiole and midrib of the lamina. In small leaves 1-3 bundles enter the base of the petiole. **Secretory cells** with unidentified contents noted at Kew in the petiolar ground tissue.

AXIS

YOUNG STEM (Fig. 11 D)

Cork said to arise in the sub-epidermis. Inner part of the primary **cortex** very lacunar; containing branched sclerenchymatous idioblasts in the intercellular spaces. **Pericycle** including an almost continuous ring of sclerenchyma, consisting mainly of fibres. **Phloem** devoid of mechanical elements in the young material examined at Kew, but secondary phloem from old bark said by Bailey and Nast (92) to include irregular masses of dense, non-fibrous, crystalliferous sclerenchyma. **Vascular bundles** more or less individually distinct in transverse sections; separated by conspicuous primary rays 1-3 cells wide, the component cells of the rays having relatively thick walls. **Xylem** consisting mostly of radially arranged tracheids with horizontal bordered pits. **Pith** including a fairly high proportion of thick-walled pitted **secretory cells**. Scattered secretory cells with gum-like contents also noted in the primary cortex. Solitary **crystals** recorded in the primary cortex, but none observed in material examined at Kew. Occasional cells containing solitary crystals noted in the region of the pericyclic fibres. **Nodal anatomy**. According to Bailey and Nast (92), in large leaves 5-7 strands enter the base of the petiole from a restricted portion of the vascular cylinder of the stem and, in smaller leaves, 1-3 bundles occur in the corresponding position.

WOOD (Fig. 7 E-F)

Vessels absent. **Parenchyma** occurring in the late wood as scattered cells and short tangential lines (Fig. 7 E). **Rays** of 2 distinct sizes, the larger up to

12 cells wide and 1–2 mm. high; uniseriates numerous, composed of upright cells; about 9 rays per mm.; heterogeneous (Kribs's Type I–II A), with up to 10 marginal rows of square or upright cells; the cells of the multiseriate parts definitely procumbent. **Tracheids** forming the greater part of the wood; with bordered pits, mostly on the radial walls, the pits in the early wood elongated (scalariform), those of the late wood circular, with slit-like apertures that sometimes exceed the borders; pits to ray cells typically circular (opposite), but sometimes transitional to scalariform in the early wood. With a sharp distinction between the thin-walled early wood tracheids and the thick-walled and radially flattened cells of the late wood.

TAXONOMIC NOTES

The affinities between *Trochodendron* and the Magnoliaceae, Winteraceae, Schisandraceae, &c., have been much discussed. The recent work of Smith, together with that of Bailey and Nast (92), indicates that whilst there is a close relationship between *Trochodendron* and *Tetracentron*, these genera are not very closely related to the Magnoliaceae, Degeneriaceae, Himantandraceae, Winteraceae, Schisandraceae, Cercidiphyllaceae, and Eucommiaceae. Whether *Trochodendron* and *Tetracentron* should be placed in the same or in 2 closely related families is a matter of opinion. The recent work of Croizat (501) indicates that there are considerable differences between the 2 genera. In Croizat's opinion the 2 genera have no 'Ranalian' affinities, but both of them are 'ultimately allied to the hamamelidoidsaxifragoid plexus'.

GENUS DESCRIBED

Trochodendron.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Bailey and Nast 92, Bailey and Thompson 99, Croizat 501, Foster 695, 696, Nast and Bailey 1581, Smith 2139, Varossieau 2324.

(ii) *On Wood Structure*

Bailey and Nast 93, Bailey and Thompson 99, Dadswell and Record 533, Kanehira 1206, 1209, McLaughlin 1466, 1467, Record 1783, 1843, 1851, Thompson 2256, Varossieau 2324, Wierletak 2422.

14. TETRACENTRACEAE

(FIG. 11 on p. 40)

SUMMARY

The family is here treated as unigeneric, and comprising the single genus *Tetracentron* as proposed by Smith (2139), the sole representative being *T. sinense* Oliv., a small tree which occurs in China and Upper Burma. As demonstrated by Bailey and Nast (92) *Tetracentron* differs from the closely related *Trochodendron* in the absence from the former of sclerenchymatous idioblasts, their place being taken by large, branched, secretory idioblasts with 'resinous' contents readily stained with Sudan IV. The **wood** exhibits the following features. **Vessels** absent. The greater part of the tissue formed

of extremely long **tracheids** with circular to scalariform pits on the radial walls. Some shorter and wider **vascular tracheids** present. **Parenchyma** diffuse. **Rays** up to 4 cells wide; markedly heterogeneous.

LEAF

Dorsiventral. **Stomata** (Fig. 11 B) confined to the lower surface; in some instances accompanied on either side by a subsidiary cell parallel to the pore, but in others surrounded by 4 or 5 well-defined subsidiary cells. (This last arrangement may be a development from the first caused by subdivision of the 2 initial subsidiary cells. Some indication that this may be so is afforded by the occasional occurrence of a single subsidiary cell on one side of a stoma and a subdivided one on the other.) Cuticle sometimes striated in the region of the stomata. **Mesophyll** consisting of 1 layer of palisade cells and a very lacunar spongy tissue below. Larger **veins** projecting considerably below the general level of the abaxial surface. Vascular bundles of the smaller veins embedded in the mesophyll, each of them partly or wholly surrounded by sclerenchyma. **Petiole** (Fig. 11 E), in transverse sections through the distal end of material examined at Kew, exhibiting a single crescent-shaped vascular strand with the ends somewhat incurved or almost meeting so as to form a cylinder. Xylem in the petiolar vascular strand consisting chiefly of radial rows of tracheids. According to Bailey and Nast (92), 3 separate bundles enter the base of the petiole. The same authors noted, in transverse sections of the petiole taken at the level of the stipular flanges, 3 conspicuous vascular strands which coalesce towards the distal end to form a single, almost closed vascular cylinder. Vascular cylinder again dividing at the base of the lamina to form the 5-7 bundles in the principal veins. **Secretory elements**. Large, branched, secretory idioblasts with 'resinous' contents readily stained in Sudan IV, noted in the leaf. These secretory elements said to be unlike the spherical secretory cells of the Winteraceae, Magnoliaceae, &c. A few solitary and clustered **crystals** noted at Kew in the 'cortical' and 'medullary' ground tissue of the petiole.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis. **Pericycle** including a composite and somewhat interrupted ring of fibres and stone cells. **Phloem** devoid of sclerenchyma in the young stems examined at Kew, but Bailey and Nast (92) refer to tangentially orientated clusters of sclerenchymatous elements in the bark of old stems. **Xylem** in the form of a continuous cylinder traversed by rays 1-3 cells wide; chiefly composed of radial rows of tracheids, somewhat angular as seen in transverse section, each element up to about 30 μ in diameter, with large, horizontal bordered pits. **Pith** composed of relatively thick-walled pitted cells, containing starch and occasional clustered **crystals**. Solitary crystals also noted in some of the pericyclic stone cells. **Secretory elements**. Numerous cells with gum-like but unidentified contents noted in the phloem of very young stems. Occasional large cells with translucent contents observed in the cortex of material cultivated at Kew. Bailey and Nast refer to large, branched, secretory idioblasts with 'resinous' contents, readily stained in Sudan IV, in the outer part of the cortex. **Nodal anatomy**. Trilacunar according to Bailey and Nast.

WOOD

Vessels absent. **Parenchyma** occurring in the late wood as scattered cells and small tangential groups of 2 or 3 cells. **Rays** up to 4 cells wide and 1.5 mm. high; uniseriate numerous and composed of square to upright cells; about 16 rays per mm.; heterogeneous, with up to 20 marginal rows of square or upright cells; the cells of the multiseriate parts square to procumbent. **Tracheids** forming the greater part of the wood; with bordered pits in the radial walls, those of the early wood elongated (scalariform), those of the late wood circular, usually with slit-like apertures that exceed the borders; pits to ray cells typically circular (opposite), but sometimes transitional to scalariform in the early wood. With a gradual change from thin walls in the early wood to moderately thick walls in the late wood; the outer rows radially flattened. Up to 4.5 mm. long (1466). **Vascular tracheids** with numerous, alternate, circular pits on both radial and tangential walls, occurring in longitudinal series; wider and shorter (0.18–1.28, mean 0.47 mm., 1466) than the other tracheids and resembling short vessel members, except for the absence of perforations; Thompson and Bailey (2256) note these cells as occurring particularly just below the internodes.

TAXONOMIC NOTES, *see under* TROCHODENDRACEAE

GENUS DESCRIBED

Tetracentron.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Bailey and Nast 92, Croizat 501, Smith 2139.

(ii) *On Wood Structure*

Bailey and Thompson 99, Kanehira 1209, McLaughlin 1466, 1467, Record 1843, Tang 2231, Thompson and Bailey 2256.

15. ANNONACEAE

(FIG. 12 on p. 46; FIG. 13 on p. 48; FIG. 14 on p. 54)

SUMMARY

(i) GENERAL

Trees, shrubs, or climbers which occur in tropical and sub-tropical regions. The **hairs** are mostly simple but stellate types and small peltate scales also occur. The cells of the **epidermis**, especially of the leaf, contain solitary or clustered **crystals** (Fig. 12 A) in several genera, their distribution being of considerable diagnostic value. **Secretory cells** are constantly present in the leaf parenchyma and sometimes in the parenchymatous tissues of the young stem as well. Stone cells, frequently in the form of **diaphragms**, are generally present in the pith, while sclerosed elements of various kinds also occur in other parenchymatous tissues of the leaf and axis.

(ii) WOOD

Vessels usually few, perforations simple, intervacular pitting alternate and usually minute to small, pits to parenchyma similar, members of medium

length. **Parenchyma** apotracheal, in numerous fine lines, sometimes with a little vasicentric in addition, often storied. **Rays** typically wide and high, with few uniseriades, 3–16 (mostly 4–8) cells wide, slightly heterogeneous to homogeneous, commonly containing oil or mucilage cells. **Fibres** with small bordered pits, of medium length.

LEAF

Generally dorsiventral, but see also below under 'Mesophyll'. **Hairs** (Fig. 12 B) mostly simple, but stellate and peltate types also occur. Cells of the lower **epidermis** provided with papillae interconnected by cuticular ridges in *Annona glauca* Schum. et Thonn., *Cleistopholis glauca* Pierre, *C. staudtii* Engl. et Diels, *Enantia kummeriae* Engl. et Diels. Epidermis multi-seriate in species of *Annona*, *Cleistopholis*, *Ellipeia*, *Miliusa*, *Mitrephora*, *Pachypodanthium*, *Xylopia*; sometimes including solitary or cluster crystals. **Stomata** rubiaceous; confined to the lower surface. **Mesophyll** in *Artabotrys suaveolens* Blume. including 2 rows of palisade cells towards the upper and 1 towards the lower surface, with spongy tissue between them. Mesophyll including fibres parallel to the surface of the leaf in certain species of *Annona*, *Anaxagorea*, *Asteranthe*, *Guatteria*, *Heteropetalum*, *Popowia*, *Sagerea*, *Unona*, *Uvaria*, and similar cells arranged vertically in *Heteropetalum brasiliense* Benth. Branched sclerenchymatous cells also recorded as frequent in *Annona*, *Duguetia*, *Guatteria*, *Habzelia*, *Unona*. **Midrib** provided with medullary bundles within a ring of collateral strands in *Cananga odorata* Hook. f. et Thoms. including a closed vascular cylinder in *Uvaria zeylanica* Linn. according to Worsdell (2469), and a V-shaped strand in *Artabotrys suaveolens*. Vascular bundles of the small **veins** vertically transcurrent. **Petiole** (Fig. 14 A–B), in transverse sections through the distal end, exhibiting an arc of widely spaced collateral bundles, the number of strands varying in different genera and species, e.g. with an arc of 3 large and several small bundles in *Monodora myristica* Dun. Additional medullary strands present in the petiole of *Cananga odorata*. According to Ozenda (1647) a single vascular arc enters the base of the petiole in most Annonaceae, the solitary arc dividing into 3 strands near the base of the petiole. Two additional lateral strands are also given off, but reunite more towards the distal end of the petiole. Transverse sections through the middle part of the petiole thus show an arc of 5 bundles, and sections through the distal end an arc of 3 bundles. *Uvaria* differs from *Annona* and related genera in having more numerous petiolar vascular strands arranged in a circle, the structure thus recalling that of the petiole of the Magnoliaceae. Large stone cells scattered in the parenchymatous tissues of the petiole in *Monodora myristica* and *Uvaria virens* N. E. Br. **Mucilage cells** recorded in certain species of *Annona*, *Rollinia*, and *Habzelia*. **Crystals** (Fig. 12 A) solitary and clustered; present especially in the epidermis and to a lesser extent in the mesophyll and around the vascular bundles of the veins. Considerable diagnostic value was attached by Solereder to the distribution of crystals in the epidermal cells, the following more or less distinct but overlapping types being recognized. (i) A single solitary or clustered crystal present in each epidermal cell. This type recorded in 182 species belonging to 25 genera, including species of *Annona*, *Artabotrys*, *Asimina*, *Bocagea*, *Duguetia*, *Goniiothalamus*, *Melodorum*, *Rollinia*, and *Stormia*. (ii) A single,

oblique, solitary crystal of variable form and size present in each epidermal cell. This type recorded in 56 species belonging to 10 genera including species of *Asimina* (1 sp.), *Duguetia* (1 sp.), *Melodorum*, *Miliusa*, and *Orophea*. (iii) A single clustered or solitary crystal confined to some of the epidermal cells, the intervening cells being filled with brown contents. (iv) A single, oblique, solitary crystal present in some but not all of the epidermal cells, the intervening cells being filled with brown contents, e.g. in *Sageraea*. (v) Epidermal crystals confined to small cells above the veins, e.g. in species of *Alphonsea*, *Ephedranthus*, and *Mitrephora*. (vi) Vascular bundles sheathed by crystalliferous cells in *Cyathocalyx* (1 sp.) and *Stelechocarpus* (1 sp.).

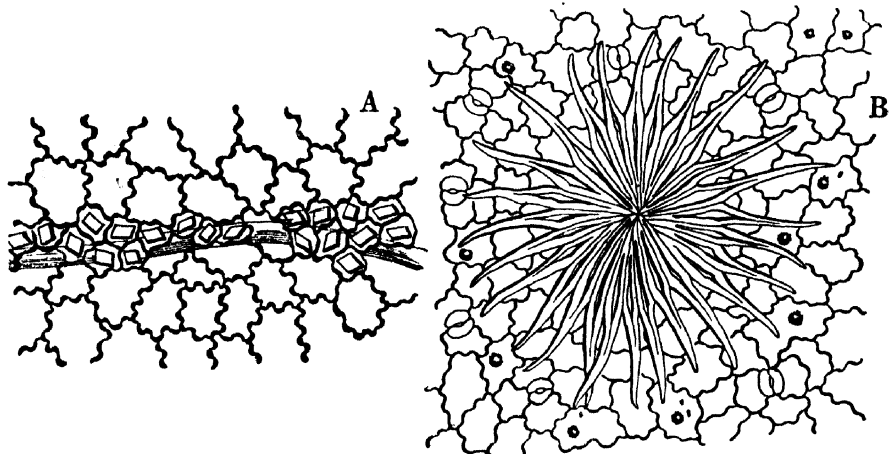


FIG. 12. ANNONACEAE

A, Epidermal crystal-cells of *Mitrephora obtusa* Hook. f. et Thoms. B, Peltate hair, with a piece of the epidermis from the lower side of the leaf of *Duguetia bracteosa* Mart.—By Solereder.

AXIS

YOUNG STEM (Fig. 14 D)

Cork arising superficially in the few examined species of *Artabotrys* (Santos, 1990), *Asimina*, *Cananga*, *Monodora*, *Stormia*, *Uvaria*. **Cortex** containing variously shaped stone cells in many species, e.g. in *Asimina triloba* Dun. and *Monodora myristica* Dun. **Pericycle** usually including strands of fibres situated externally to the phloem. **Phloem**, in transverse sections, appearing as triangular groups with the broad portions directed towards the interior; becoming stratified owing to the development of tangential groups of fibres. Portions of the rays between the phloem groups also triangular, but with inwardly directed apices. **Xylem** generally in the form of a closed ring traversed by narrow rays, but sometimes interrupted by the conspicuous and relatively broad primary rays; including vessels with simple perforations. The fine tangential lines of apotracheal parenchyma, present in the mature secondary xylem (see 'Wood' below), are not always well defined in the young stem. **Pith** segmented by diaphragms of stone cells in all examined members of the family except species of *Asimina* and *Monodora*. Small plates of stone cells sometimes occur sporadically in the pith even in the absence of complete septa. **Secretory cells**, with tanniniferous contents, common in the cortex.

WOOD (Fig. 13 A-F)

Vessels very small (less than 50 μ mean tangential diameter), e.g. in some species of *Alphonseopsis*, *Malmea*, *Orophea*, *Oxandra*, and *Popowia*, to large (more than 200 μ), e.g. in some species of *Cananga*, *Cleistopholis*, *Guattaria*, *Leptopoda*, *Rollinia*, and *Unona*; solitary and in short multiples, often with some radial pattern owing to the arrangement of the solitary and paired vessels between the large rays; radial multiples of 4 or more cells moderately common in *Goniothalamus* p.p. and *Hornschuchia* and with numerous clusters and a tendency to an ulmiform pattern in the late wood of *Asimina*; 1-45 per sq. mm.; fewest (2 or less per sq. mm.) in the species with large vessels and in some species of *Platymitra*, *Unonopsis*, and *Xylopia*; most numerous (30 or more per sq. mm.) in some species of *Malmea* and *Oxandra*; ring-porous in *Asimina* and semi-ring-porous in *Pachypodanthium*; spiral thickening reported (1886) in *Asimina*. Perforations simple, horizontal to slightly oblique. Intervascular pitting typically alternate, but, according to Record and Hess (1886), sometimes opposite, e.g. in *Cymbopetalum*; minute to moderate-sized; vessels seldom touching the rays, and pits to ray cells very rare; pits to parenchyma cells similar to the intervacular pitting, sometimes unilaterally compound (533) and occasionally with coalescent apertures, e.g. in *Anaxagorea acuminata* St. Hil.; without pits to fibres (1154). Solid deposits often present; calcium carbonate observed by Molisch in *Annona laevigata* Mart. Mean member length 0.3-0.6 mm. **Parenchyma** apotracheal, in numerous, closely spaced, fine lines, usually uniseriate, sometimes 2 or 3 cells wide (Fig. 13 A and D) and often reticulate; the cells often disjunctive with very distinctly grouped pits in the radial walls; vasicentric parenchyma in addition sometimes present in the genera with larger vessels, but rather sparse. Storied in *Annona* p.p., *Asimina*, *Cyathocalyx*, *Goniothalamus*, *Heteropetalum*, *Hexalobus*, *Miliusa*, *Monodora*, *Popowia*, and *Rollinia*, and rather vaguely storied in *Cleistopholis*, *Guatteria*, *Mitrephora*, *Polyalthia*, and *Stenanthera*. Large, thin-walled mucilage cells present in *Cananga* and *Cymbopetalum* (1886). Strands usually of 4 to 8 cells, but strands of 2 cells sometimes numerous, e.g. in *Asimina* and *Hornschuchia*. **Rays** typically wide and high; most commonly up to 4-8 cells wide, but rays up to 13-15 cells wide recorded (1886) in *Anaxagorea*, *Annona*, *Guatteria*, and *Stenanona* and only 3-4 cells wide in some species of *Alphonsea*, *Cymbopetalum*, *Disepalum*, *Diclinanona*, *Fissistigma*, *Hornschuchia*, and *Malmea*; up to 6 mm. high in some species, the larger rays often showing evidence of dissection into smaller units; uniseriates typically very few and sometimes extremely few, e.g. in some species of *Cleistopholis*, *Hexalobus*, *Monodora*, *Pachypodanthium*, *Popowia*, and *Unona*, though moderately numerous in some species of *Cyathocalyx*, *Heteropetalum*, *Oxandra*, and *Uvaria*, and usually composed of mixed upright and procumbent cells, with the latter predominating, but sometimes wholly of either procumbent or square cells. Rays 2-9, mostly 3-5, per mm. Cells often very irregular in size as seen in tangential sections (Fig. 13 C), with occasional rows of large, almost square cells interspersed among the smaller procumbent cells, e.g. in some species of *Bocagea*, *Griffithia*, *Griffithianthus*, and *Polyalthia*. Typically almost or quite homogeneous (Kribs's Types I and II), though sometimes distinctly heterogeneous, e.g. in *Miliusa velutina* Hook. f. et Thoms.; with marked differences in the size and shape of the procumbent cells even in species of the

same genus, possibly associated with differences in habit; sometimes with very narrow procumbent cells, from which occasional marginal rows may stand out as distinctly higher; sometimes composed almost entirely of large,

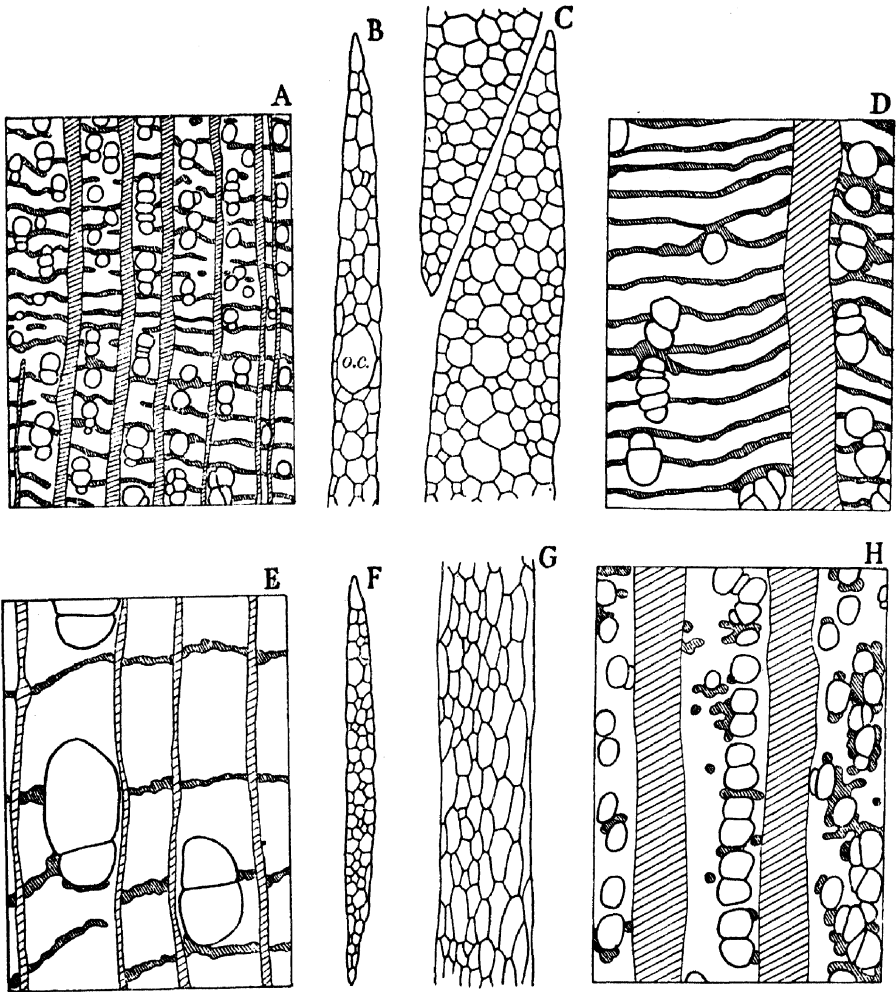


FIG. 13. ANNONACEAE, A-F; EUPOMATIACEAE, G-H

A, *Oxandra lanceolata* Baill. B, *Aberemoa asterotricha* Diels, with large oil cell. C, *Griffithianthus fuscus* Merrill. D, *Anaxagorea acuminata* St. Hil. E, *Xylopia ferruginea* Baill. F, *Alphonsea maingayi* Hook. f. et Thoms. G, *Eupomatia laurina* R. Br. H, *E. laurina* R. Br. O.C., Oil or mucilage cell.

nearly square, cells, from which the marginal rows are not very clearly distinguished in tangential section. The rays with small procumbent cells sometimes homogeneous, e.g. in *Duguetia*, *Hexalobus*, *Rollinia*, and *Stenanthera*. Typically without crystals, but with numerous, small crystals in some species of *Alphonseopsis*, *Goniiothalamus*, and *Hornschuchia*; Gonggrijp (794) reports silica in *Cyathocalyx*. Oil or mucilage cells scattered irregularly among the

ray cells in *Aberemoa* (Fig. 13 B), *Cananga* (1154), *Cleistopholis*, *Cyathocalyx* p.p., *Cymbopetalum* (1886), *Diclinanona*, *Duguetia*, *Mezzettia*, *Monodora*, *Pachypodanthium*, and *Unona*. **Fibres** with small, but often distinctly bordered pits, which are equally numerous on both radial and tangential walls; the borders about the same size or slightly larger than those of the intervacular pitting. Walls thin to moderately thick. Mean length 0.9–1.5 mm.

TAXONOMIC NOTES

It is interesting to note that the secretory cells in the leaf of the Annonaceae are of the same type as those found in the Magnoliaceae. Worsdell (2469) has stated his opinion that the vascular structure of Annonaceae recalls that of the Magnoliaceae and *Paeonia* spp.

The wood anatomy of the family is very uniform, and the genera, with the exception of *Asimina*, are not easily distinguishable. The simple perforations and mean member length of the vessels, the frequently storied parenchyma and the scarcity of uniseriate rays all indicate a moderately high level of specialization.

ECONOMIC USES

The Custard Apple is *Annona reticulata* Linn. *Artabotrys suaveolens* Blume from the Philippine Islands contains an alkaloid which may be of medicinal value. *Artabotrys odoratissimus* R. Br., from India and Ceylon, is cultivated for its fragrant flowers. *Cananga odorata* Hook. f. et Thoms. is used for perfumery purposes. The aromatic and pungent fruits of *Xylopia aethiopica* A. Rich are used by West African natives as a condiment and in medicine.

Lancewood, *Oxandra lanceolata* (Sw.) Baill. is the only timber of commercial importance. Schneider (2044) notes that in the Philippines some species are used locally for house-building, but are not distinguished commercially. Pearson and Brown (1679) include 3 genera among the commercial timbers of India, *Milusa*, used for tool handles, oars, &c., *Polyalthia*, used for matches and packing-cases, and *Sageraea*, used for bentwood and tool handles.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aberemoa, *Anaxagorea*, *Annona*, *Artabotrys*, *Asimina*,* *Asteranthe*, *Cananga*,* *Cleistopholis*, *Duguetia*, *Ellipeia*, *Guatteria*, *Habzelia*, *Heteropetalum*, *Milusa*, *Mitrephora*, *Monodora*,* *Pachypodanthium*, *Rollinia*, *Stormia*, *Unona*, *Uvaria*,* *Xylopia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Aberemoa, *Alphonsea*, *Alphonseopsis*, *Anaxagorea*, *Annona*, *Asimina*, *Bocagea*, *Brieya*, *Cananga*, *Cleistopholis*, *Cyathocalyx*, (*Cymbopetalum*), *Dennettia*, (*Diclinanona*), *Disepalum*, *Drepananthus*, *Duguetia*, *Enantia*, *Fissistigma*, *Goniiothalamus*, *Griffithia*, *Griffithianthus*, *Guamia*, *Guatteria*, *Heteropetalum*, *Hexalobus*, *Hornschuchia*, *Malmea*, *Meiogyne*, *Mezzettia*, *Milusa*, *Mitrephora*, *Monodora*, *Orophea*, *Oxandra*, *Oxymitra*, *Pachypodanthium*, *Platymitra*, *Polyalthia*, *Popowia*, *Rollinia*, *Saccopetalum*, *Sageraea*, *Sapranthus*, *Stelechocarpus*, *Stenanona*, *Stenanthra*, (*Trivalvaria*), *Unona*, *Unonopsis*, *Uvariastrium*, *Uvariadendron*, *Xylopia*.

LITERATURE

(i) *On General Anatomy*

Ozenda 1647, Santos 1990, Worsdell 2469.

(ii) *On Wood Structure*

Bastos 147, Benoist 169, den Berger 179, 182, 183, Besson 186, Burgerstein 310, Cooper and Record 461, Coster 481, Dadswell and Record 533, Desch 574, Garratt 747, 747A, Gonggrijp 794, Hess 963, Hopkinson 1083, Howard 1088, Janssonius 1154, Jentsch 1175, 1177, Jones 1191, Kanehira 1206, 1209, 1214, Kribs 1283, Lecomte 1334, Normand 1607, Pearson and Brown 1679, Pereira 1687, Pfeiffer, H. 1712, Pfeiffer, J. Ph. 1713, Record 1783, 1790, 1818, 1843, 1851, Record and Hess 1886, Riera 1937, Stone 2202, 2207, Tupper 2295, Williams 2430.

16. EUPOMATIACEAE

(FIG. 13 on p. 48; FIG. 14 on p. 54)

SUMMARY

(i) GENERAL

A family of Australian shrubs included in the single genus *Eupomatia*. The rubiaceous **stomata** in the leaf and **secretory sacs** in the pith of the young axis are two of the most significant anatomical features.

(ii) WOOD

Vessels small, with a radial pattern, perforation plates scalariform, intervascular pitting scalariform to opposite; members very long. **Parenchyma** rather sparse, diffuse, and paratracheal. **Rays** very broad and high, with sheath cells. **Fibres** septate, of medium length to moderately long.

LEAF

Weakly dorsiventral; almost glabrous. Cells of the **epidermis** with straight or somewhat curved anticlinal walls; those of the lower epidermis with rather more sinuous anticlinal walls. **Stomata** confined to the lower surface; always rubiaceous, but sometimes with more than one pair of subsidiary cells parallel to the pore. **Mesophyll** including a single layer of very short palisade cells, the remainder consisting of homogeneous, somewhat spongy parenchyma. **Midrib** including a deep, crescent-shaped vascular strand strongly supported by sclerenchyma on the adaxial side and between the arms of the crescent. Vascular bundles of the smaller **veins** embedded in the mesophyll. **Petiole** (Fig. 14 c), in transverse sections through the distal end, exhibiting a deep crescent of widely spaced vascular bundles, with a group of stone cells in the centre of the petiole between the arms of the vascular crescent. Ozenda (1647) observed 7 vascular strands in the base of the petiole, and concluded that the nodal structure resembles that of the Magnoliaceae. **Secretory cells** with amorphous contents scattered in the ground tissue of the petiole, and a few secretory idioblasts, sometimes with yellowish granular contents, scattered throughout the mesophyll. Ground tissue of the petiole also including small cluster **crystals**.

AXIS

YOUNG STEM (Fig. 14 E)

Epidermis with very thick cuticle. **Cork** formation not seen in material examined by the author. Outer part of the primary **cortex** collenchymatous. **Pericycle** including well-developed but widely spaced groups of fibres with wide lumina. **Phloem** and **xylem** traversed by relatively broad rays. **Pith** wide, composed of large, thin-walled parenchymatous cells, but supported by a few scattered stone cells. **Secretory elements**. Somewhat elongated secretory cells with amorphous contents present in the cortex, and smaller more numerous ones in the phloem. Elongated, slightly sinuous, secretory sacs with amorphous contents, each sac surrounded by small parenchymatous cells, present in the pith. Small cluster **crystals** abundant in the ground tissue of the very young stem.

WOOD (Fig. 13 G-H)

Vessels small (mean tangential diameter about $70\ \mu$), solitary and in short to long radial multiples, which often give a distinct radial pattern (Fig. 13 H). Perforation plates scalariform, with many fine bars (20 to more than 100). Intervascular pitting small to moderate-sized, opposite or scalariform; pits to ray cells similar. Mean member length about 1.2 mm. **Parenchyma** rather sparse, diffuse, and scanty paratracheal (Fig. 13 H). **Rays** of 2 distinct sizes, the larger up to 12, usually 6 to 9, cells wide and up to 5 mm. high; uniseriate rays rather few and low, composed of high upright cells; about 10 rays per mm.; multiseriate rays composed almost entirely of square and upright cells; sheath cells usually present, sometimes very high. **Fibres** with simple or indistinctly bordered (747) pits, septate and with moderately thick walls. Mean length about 1.6 mm.

TAXONOMIC NOTES

Although *Eupomatia* has features in common with the Annonaceae it is generally treated as the only genus in a distinct family. Both Garratt (747) and Lemesle (1353) consider that differences in the wood structure support this separation. Lemesle concludes from the anatomy of the wood and the floral morphology that the Eupomatiaceae are among the most primitive of angiosperms, more primitive even than the Magnoliaceae.

GENUS DESCRIBED

Eupomatia.*

* Represented in the Kew slide collection.

The above description of the general anatomy is based on material of *E. bennettii* F. Muell. cultivated at Kew.

LITERATURE

(i) *On General Anatomy*

Lemesle 1354, Ozenda 1647.

(ii) *On Wood Structure*

Garratt 747, Lemesle 1353, Record 1843, 1851.

17. MENISPERMACEAE

(FIG. 14 on p. 54; FIG. 16 on p. 60; FIG. 91 on p. 402.)

SUMMARY

(i) GENERAL

The family includes shrubs and small trees but most members are lianes. It occurs chiefly in tropical and sub-tropical regions. The **vascular bundles** in young stems are individually distinct even with the naked eye, being separated by the broad primary medullary rays which may be lignified or unlignified. In the **xylem**, the vessels have wide lumina, and simple perforations, whilst the ground tissue consists of prosenchymatous elements with bordered pits. The **pericycle** includes an undulating, generally continuous ring of sclerenchyma formed from arcs of fibres, belonging to the separate bundles, with groups of stone cells between them. **Anomalous secondary thickening** is very common, and is due to the formation from extrafascicular cambia, of one or more concentric or eccentric rings of bundles. (For further details see under 'Wood'.) **Crystals** of calcium oxalate are common, and may be solitary, clustered, or secreted in the form of raphides, styloids, and crystal-sand. **Secretory sacs**, with various kinds of contents, are characteristic of certain genera, whilst idioblasts and other types of isolated sclerenchymatous elements also occur. **Hairs** include the following kinds. (i) Uniseriate, consisting of 2 or more cells. (ii) Glandular types, which may be shaggy, long and uniseriate or small. (iii) Unicellular, ellipsoidal, or club-shaped. The **stomata** are very variable, especially in the nature of the surrounding epidermal cells, and no single type can be regarded as typical of the family as a whole.

(ii) WOOD

Woods typically with **included phloem** of the 'concentric' type. **Vessels** very small to medium-sized, nearly all solitary and seldom touching the rays, perforations simple, intervascular pitting alternate, pits to parenchyma similar or elongated and grouped, members of medium length to moderately short. **Parenchyma** (a) conjunctive, (b) apotracheal, diffuse or in short bands. **Rays** interfascicular only. **Fibres** with numerous bordered pits, of medium length.

LEAF

Generally dorsiventral; centric in *Cocculus laevis* DC. according to Beauquesne (162).

Hairs. (i) Uniseriate, bicellular, in species of *Abuta*, *Adeliopsis*, *Albertisia*, *Antizoma*, *Bania*, *Carronia*, *Chondodendron*, *Cissampelos*, *Cocculus*, *Cyclea*, *Detandra*, *Husemannia*, *Hyperbaena*, *Limacia*, *Macrococculus*, *Menispermum*, *Pachygone*, *Paraphora*, *Pericampylus*, *Pleogyne*, *Pycnarrhena*, *Sciadotenia*, *Syrrhonema*, *Tiliacora*. (ii) Uniseriate, of more than 2 cells, in species of *Anamirta*, *Arcangelisia*, *Calycocarpum*, *Chasmanthera*, *Coscinium*, *Disciphania*, *Heptacyclum*, *Menispermum*, *Parabaena*, *Stephania*, *Tinospora*. (iii) Small, unicellular, ellipsoidal or club-shaped glandular hairs, in species of *Kolobopetalum*, *Miersiophyton*, *Tinospora*. (iv) Long, uniseriate glandular hairs, in

species of *Calycarpum*, *Parabaena*. (v) Shaggy glandular hairs recorded in *Jateorhiza*.

Epidermis. (i) Cells specially large in species of *Cocculus*. (ii) Cells partly sclerotic in *Anomospermum reticulatum* Eichl., *Hyperbaena laurifolia* Urb., *Triclisia loucoubensis* Baill. (iii) Papillose: (a) on both surfaces in *Cissampelos capensis* Thunb., *C. pareira* Linn. (sometimes), *Cocculus laeaba* DC. and *Stephania rotunda* Lour; (b) on the lower surface only, in some instances confined to isolated cells above the veins, in *Cissampelos fluminensis* Eichl., *C. glaberrima* St. Hil., *Hypsipodes subcordatus* Miq., *Jateorhiza columba* (Lam.) Miers., *Menispermum canadense* Linn., *M. dauricum* DC., *Stephania abyssinica* Walp. **Stomata** exhibiting no characteristic structure; generally confined to the lower surface, but recorded on both surfaces in species of *Antizoma* and in *Cocculus cebatha* DC. Rubiaceous in *Cocculus carolinus* DC. and *C. laurifolius* DC. Rosettes of subsidiary cells recorded in certain species of *Albertisia*, *Anamirta*, *Bania*, *Burasaia*, *Carronia*, *Cocculus*, *Cyclea*, *Fawcettia*, *Heptacyclum*, *Husemannia*, *Hyperlaena*, *Leichardtia*, *Limacia*, *Macrococculus*, and thin-walled subsidiary cells in *Chlaenandra*. Subsidiary cells narrow in *Parabaena*, *Pleogyne*, *Pycnarrhena*, *Sarcopetalum*. Stomata in groups in *Macrococculus pomiferus* Becc., *Antizoma* spp. **Hydathodes** recorded by Engler (632) in *Anamirta* and related genera. **Hypoderm** mucilaginous in certain species of *Adeliopsis*, *Anomospermum*, *Cissampelos*, *Cyclea*, *Limacia*, *Stephania*. **Mesophyll**. Thickenings or swellings present on the cell walls in *Adeliopsis*, *Canonia*, *Cissampelos*, *Cocculus*, *Cyclea*, *Limacia*, *Pachygone*, *Pericampylus*, *Stephania*, *Syrrhonema*. Spongy mesophyll partly or wholly composed of thick-walled, generally lignified cells, e.g. in *Albertisia papuana* Becc., *Anamirta cocculus* Wight et Arn., *Husemannia protensa* F. v. Müll., *Parabaena sagittata* Miers. Idioblasts or similar isolated sclerosed cells recorded in *Abuta concolor* Poepp. et Endl., *Chlaenandra ovata* Miq., *Chondodendron platyphyllum* Miers., *Coscinium bluneanum* Miers., *Detandra paraensis* Eich. 'Spicular cells' of various types present in *Adeliopsis decumbens* Benth., *Anamirta cocculus*, *Anomospermum japurense* Eich., *Arcangelisia lemniscata* Becc., *Burasaia congesta* Decne., *B. gracilis* Decne., *B. madagascariensis* DC., *Heptacyclum zenkeri* Engl., *Limacia cuspidata* Hook. f. et Th., and *L. microphylla* Miers.

Vascular bundles of the **veins** generally accompanied by sclerenchyma except in certain species of *Antizoma*, *Cissampelos*, *Desmonema*, *Diploclisia*, *Disciphania*, *Miersiophyton*, *Stephania*, *Tinospora*. Lateral and smaller veins vertically transcurrent in species of *Abuta*, *Anomospermum*, *Coscinium*, *Hyperbaena*, *Limacia*, *Macrococculus*, *Menispermum*, *Pachygone*, *Paraphora*, *Pericampylus*, *Pycnarrhena*, *Sarcopetalum*, *Triclisia*.

Transverse sections through the central portion of the **petiole** (Fig. 14 F) exhibiting a ring of isolated bundles in certain species of *Anamirta*, *Arcangelisia*, *Cissampelos*, *Cocculus*, *Coscinium*, *Fibraurea*, *Limacia*, *Menispermum*, *Pachygone*, *Pycnarrhena*, *Stephania*, *Tiliacora*, *Tinomisium*, *Tinospora*. Swellings sometimes present at the distal and basal ends of the petiole or at the distal end only. Anatomical structure of the swollen regions differing from that of the remainder of the petiole. No correlation was found by Rudolph (1966) to exist between species resembling one another in respect of the structure of these swellings and those resembling one another in fruit and seed structure.

Crystals secreted in the form of needles, prisms, rhombohedra, solitary types or clusters, raphides and crystal-sand. (i) Large solitary crystals recorded in *Aspidocarya*, *Burasaia*, *Chasmanthera*, *Chlaenandra*, *Fawcettia*, *Hypsipodes*, *Kolobopetalum*, *Leichardtia*, *Syntriandrium*, *Tinospora*. (ii) Small

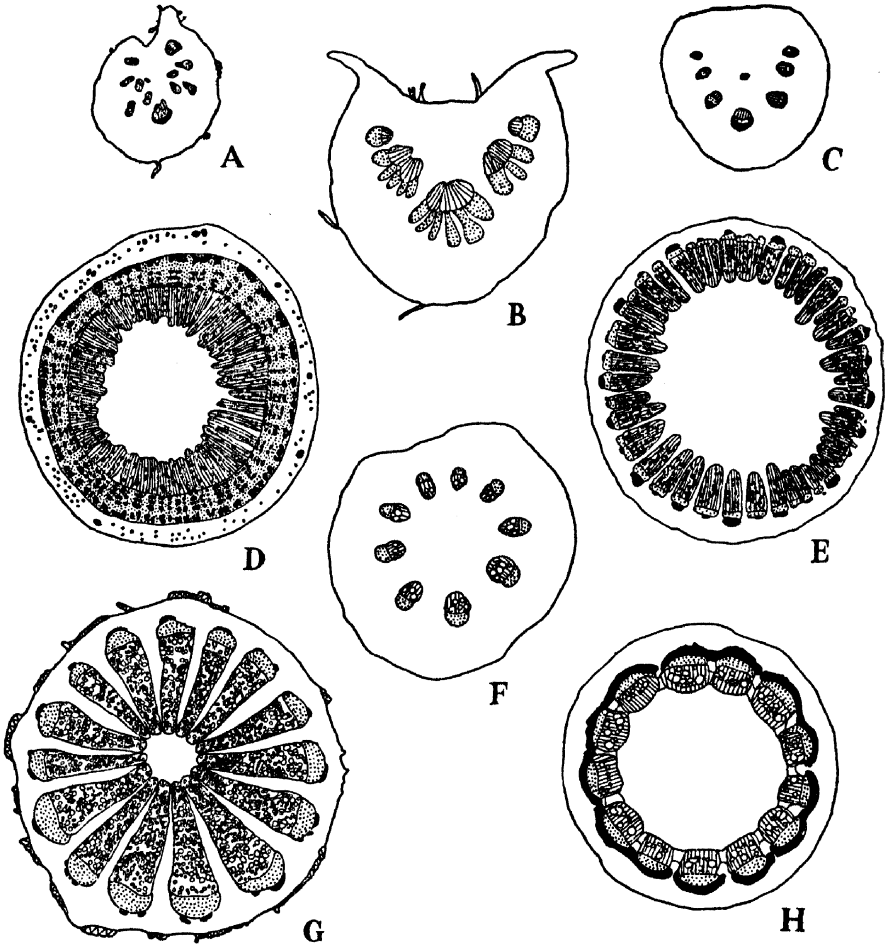


FIG. 14. ANNONACEAE, A-B and D; EUPOMATIACEAE, C and E; MENISPERMACEAE, F-H

A, *Cananga odorata* Hook. f. et Thoms. Petiole $\times 9$. B, *Asimina triloba* Dun. Petiole $\times 15$. C, *Eupomatia bennettii* F. Muell. Petiole $\times 8$. D, *Monodora myristica* Dun. Stem $\times 7$. E, *Eupomatia bennettii* F. Muell. Stem $\times 8$. F, *Stephania rotunda* Lour. Petiole $\times 33$. G, *Menispermum canadense* Linn. Stem $\times 5$. H, *M. canadense* Linn. Young stem $\times 15$.

rhombohedral crystals in *Abuta*, *Anomospermum*, *Burasaia*, *Heptacyclum*, *Husemannia*, *Hyperbaena*, *Limacia*, *Macrocculus*, *Pachygone*, *Pleogyne*, *Pycnarrhena*, *Tiliacora*; said to be particularly abundant in epidermis of *Anamirta cocculus* Wight et Arn., *Desmonema* and *Tiliacora warneckeii* Engl. (iii) Styloid-shaped or prismatic crystals recorded in *Cissampelos*, *Cyclea*, *Diploclisia macrocarpa* Miers., *Jateorhiza columba* (Lam.) Miers., *Pericampylus*

incanus Miers., *Stephania*. (iv) Large styloid-like, geniculate, hemitropic crystals present in *Leichardtia clamboides* F. v. Müll. (v) Large cluster crystals recorded in *Chondodendron platyphyllum* Miers. (vi) Small cluster crystals in *Macrococculus pomiferus* Becc. and *Pericampylus incanus* Miers. (vii) Raphides recorded by Santos (1992) in *Anamirta cocculus* Wight et Arn. and *Arcangelisia flava* (Linn.) Merrill. (viii) Paired crystal cells occur in *Leichardtia clamboides*. (ix) Sphaero-crystalline masses of an unknown chemical substance recorded in the lower epidermis of *Cocculus laurifolius* DC. and *Sarcopetalum harveyanum* F. v. Muel.

Secretory sacs in the lamina generally occur in association with the sclerenchyma of the veins; comparatively rare in the mesophyll. Secretory sacs also present in the petioles as well as in the axis. (They are believed, according to Solereder and to Santos (1992), to arise from vertical rows of cells of which the transverse walls break down, but this view has been disputed by Beauquesne (162), who considers them to be truly unicellular. Nature of the contents very variable.)

(i) Elongated sacs with yellowish or brown contents recorded in *Albertisia*, *Anamirta*, *Burasaia*, *Chasmanthera*, *Cissampelos*, *Cocculus*, *Desmonema*, *Disciphania*, *Fawcettia*, *Hypsipodes*, *Jateorhiza*, *Kolobopetalum*, *Limacia*, *Parabaena*, *Syntriandrium*, *Tiliacora*, *Tinospora*. (ii) Short sacs with reddish-brown contents said to occur in '*Antizoma calcarifera* Miers.', '*A. lycioides* Miers.', *Cissampelos fasciculata* Benth., *C. pareira* Linn., *Diplochlisia macrocarpa* Miers., *Tiliacora racemosa* Colebr., *Trichlisia loucoubensis* Baill. Secretory receptacles of intercellular origin and often enclosed by the arc-shaped cells of the spongy tissue, recorded in *Anomospermum japurense* Eichl. and *Tinospora bakis* Miers.

Rosettes of **silicified cells** present in *Coscinium blumeianum* Miers. Silicious contents recorded in tubular cells at the ends of the smaller veins of *Arcangelisia lemniscata* Becc. **Berberin** recorded in *Coscinium fenestratum* Colebr., *Jateorhiza palmata* (Lam.) Miers., *Menispermum canadense* Linn.

AXIS

YOUNG STEM (Fig. 14 G-H)

Cork formation observed in only a few species; developing very late in *Menispermum canadense* Linn. According to Möller, as cited by Solereder, cork formation in this species is at first superficial and confined to certain areas of the stem, 'and then spreads peripherally as it penetrates deep into the cortex'. Primary **cortex** sometimes including groups of stone cells, e.g. in *Anamirta cocculus* Wight et Arn. **Pericycle** including crescents of fibres opposite and often in contact with the phloem strands, but fibres sometimes becoming united by stone cells to form a composite, continuous, sinuous ring of sclerenchyma. Composite ring said by Solereder to persist in thick stems of *Cissampelos pareira* Linn. and *Hyperbaena domingensis* Benth., but the arcs of fibres become split into groups separated from one another by stone cells in the last of these species. **Vascular bundles** separated by broad, lignified or unlignified primary medullary rays. Vessels large and conspicuous, with simple perforations. **Pith** generally broad. Inner part, e.g. according to Solereder in *Anamirta cocculus*, *Coscinium blumeianum* Miers. and *Limacia*

velutina Miers., consisting of empty cells, but peripheral part composed of vertically elongated, pitted cells, sometimes with thin transverse septa. Fibrous cells resembling phloem fibres sometimes present on the inner side of the groups of primary xylem, especially in species, e.g. *Aspidocarya uvifera* Hook. f. et Thoms. and *Cocculus laurifolius* DC., which exhibit no clear differentiation between the inner and outer part of the pith. **Crystals** and **secretory sacs** of the same types as described under 'Leaf'.

WOOD¹ (Figs. 16 D and F and 91 A)

Vessels small (mean tangential diameter less than 100 μ) to medium-sized (100–200 μ), and occasionally very small (25–50 μ), e.g. in *Cocculus*; mostly solitary, but occasionally in tangential groups of 2–4, which may give a tangential pattern, e.g. in *Tiliacora glycosmantha* Diels.; 5–40 per sq. mm.; seldom in contact with the rays. Perforation plates simple, slightly oblique. Intervascular pitting rather scarce, alternate and moderate-sized; pits to parenchyma usually round with slit-like apertures, but, particularly at the ends of the vessel members, sometimes large, irregular in shape and elongated, simple or with narrow borders, a cluster of such pits often resembling an irregular scalariform perforation plate. Myers (1577) has described thick-walled and pitted tyloses in *Menispermum*. Mean member length 0.3–0.45 mm. **Parenchyma** (a) conjunctive, between the successive layers of xylem and phloem bundles, and including layers of isodiametric or radially elongated stone cells, the layers usually 2–3 cells wide, but often wider between the phloem strands; sometimes containing numerous crystals; (b) apotracheal, diffuse, and in short tangential lines; strands usually of 2–4 cells. **Rays** interfascicular only, and usually not continuous radially from one layer of bundles to the next. Up to 10–23 cells wide and usually extremely high; cells all slightly procumbent to all square, with little distinction between central and marginal cells, and sometimes almost homogeneous. **Fibres** with numerous, distinctly bordered pits on both radial and tangential walls; pits to vessels similar, but more numerous; such cells often have wider lumina and are irregular in shape (especially in *Abuta* and *Tiliacora*) and could possibly be classified as vasicentric tracheids; walls moderately thick. Mean length 1.1–1.2 mm. **Included (interxylary) phloem** (Figs. 91 A and 16 D and F) of the 'concentric' type (*c.l. circumvallatum*) observed or reported (85, 1712, 1851, 2158) in *Abuta*, *Anomospermum*, *Cebatha*, *Chasmanthera*, *Chondodendron*, *Cissampelos*, (Root), *Clyphea*, *Cocculus*, *Disciphania*, *Jateorhiza*, *Menispermum*, *Pachygonia*, *Pericampylus*, *Telitoxicum*, and *Tiliacora*. The anomaly consists of successive bundles of xylem and phloem repeating the structure of the young stem; the bundles separated by tangential bands of parenchyma and large interfascicular rays. Solereder lists the following lianes as having normal structure: species of *Anamirta*, *Cissampelos*, *Cocculus*, *Coscinium*, *Jateorhiza*, *Menispermum*, and *Tinospora*.

RHIZOME

With a stele consisting of a single ring of bundles surrounded by a ring of sclerenchyma in *Menispermum canadense* Linn.

¹ Based entirely on material with anomalous structure.

ANOMALOUS STRUCTURE, *see under* 'WOOD'

ROOT

In *Cocculus leaeba* DC. and '*Tinospora tuberculata* Beauf.' described by Beauquesne (162) as somewhat resembling the aerial stem, but with the **xylem** groups of the bundles united at the centre, thereby practically or completely obliterating the pith, and giving the xylem a stellate appearance, with phloem at the ends of the radii. For root structure of *Jateorhiza palmata* (Lam.) Miers. *see* 'Economic Uses'.

TAXONOMIC NOTES

The general stem structure, with the separate vascular bundles, suggests that the members of this family have affinities with the woody genera of the Berberidaceae. This is also confirmed by the occurrence of berberin in certain genera of Menispermaceae. In the respective systems of Bentham and Hooker, Engler, and Hutchinson, the Menispermaceae are placed close to the Berberidaceae. This shows that the vegetative anatomy and the floral structure both point to the same conclusion concerning the affinities of this family. Garratt (747) states that the wood anatomy of this family indicates that it has no affinity with the Myristicaceae.

ECONOMIC USES

The sliced root of *Jateorhiza palmata* (Lam.) Miers., which is known commercially as Calumba or Colombo Root, is used medicinally for treating indigestion. Commercial samples of Calumba Root consist of thick slices about 2–6 cm. in diameter, somewhat depressed at the centre and covered externally by a thin, brownish, wrinkled layer of cork. The greater part of the ground tissue of the root is composed of parenchyma with abundant starch. Other diagnostic characters include groups or a loose ring of yellow, thick-walled, pitted stone cells in the outer cortical tissues; prismatic crystals in some of the stone cells; phloem in the form of narrow, radiating groups of somewhat disorganized, un lignified tissue; radial groups of wide xylem vessels with yellowish walls, embedded in parenchymatous ground tissue; more irregularly distributed vessels towards the centre of the root. The walls of the stone cells, and to a lesser extent of the xylem elements, are coloured green on treatment with 60 per cent. sulphuric acid.

The root of *Chondodendron tomentosum* Ruiz. et Pav. known as 'Pareira brava', has tonic and diuretic properties. The fruits of *Anamirta paniculata* Colebr. are used in the preparation of ointments.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abuta, Adeliopsis, Albertisia, Anamirta, Anomospermum, Antizoma, Arcangelisia, Aspidocarya, Bania, Burasaia, Calycarpum, Carronia, Chasmanthera, Chlaenandra, Chondodendron, Cissampelos, Cocculus,* Coscinium, Cyclea, Desmonema, Detandra, Diploclesia, Disciphania, Fawcettia, Heptacyclum, Husemannia, Hyperbaena, Hypsipodes, Jateorhiza, Kolobopetalum, Leichardtia, Limacia, Macrocculus, Menispermum,* Miersiophyton, Pachygone, Parabaena, Paraphora, Pericampylus, Pleogyne,

Pycnarrhena, *Sarcopetalum*, *Sciadotenia*, *Sinomenium*,* *Stephania*,* *Syntriandrium*, *Syrrhonema*, *Tiliacora*, *Tinomiscium*, *Tinospora*, *Triclisia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Abuta, *Chondodendron*, *Cocculus*, *Hyperbaena*, (*Menispermum*), *Teliotoxicum*, *Tiliacora*.

LITERATURE

(i) On General Anatomy

Beauquesne 162, Engler 632, Fiebrig 684, Holm 1066, 1073, Myers 1577, Rudolph 1966, Sabnis 1977, Santos 1989, 1992, Shirley and Lambert 2089, Short 2093.

(ii) On Wood Structure

Chalk and Chattaway 362, Dadswell and Record 533, Garratt 747, Janssonius 1154, Myers 1577, Pfeiffer, H. 1712, Record 1843, 1851, Record and Hess 1886, Williams 2430.

18. BERBERIDACEAE

(FIG. 15 on p. 58; FIG. 16 on p. 60; FIG. 17 on p. 65)

SUMMARY

(i) GENERAL

A family occurring chiefly in North Temperate regions and consisting partly of herbs with rhizomes and partly of shrubs which are usually spiny.

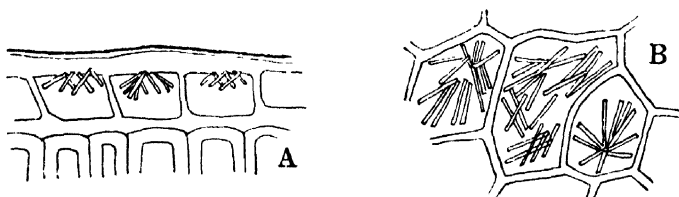


FIG. 15. *BERBERIDACEAE*

A-B, Crystals in the upper epidermis of the leaf of *Mahonia japonica* DC. (after Vesque).

The spines of *Berberis* are mainly composed of sclerenchymatous fibres. In transverse sections of young internodes of the woody genera the **vascular bundles** are separated by the broad primary medullary rays, whilst a ring of fibres, believed to be pericyclic in origin, forms a tube at the periphery of the stem. In the aerial stems of the herbaceous or semi-herbaceous genera, *Achlys*, *Diphylleia*, *Epimedium*, *Hydrastis*, *Jeffersonia*, *Leontice*, *Podophyllum*, and *Vancouveria*, on the other hand, the bundles are widely spaced and generally scattered. A somewhat intermediate type is represented by *Nandina domestica* Thunb. because it possesses a ring of widely spaced bundles surrounding a large pith which occupies most of the cross-sectional area of an old stem. The structure of the individual vascular bundles recalls that of the bundles in the monocotyledons. The **stomata** are generally ranunculaceous. The tissues are frequently coloured yellow by the presence of **berberin**. Solitary or cluster **crystals** of calcium oxalate often occur.

(ii) WOOD

Vessels very small and usually with some ulmiform or radial pattern, occasionally ring-porous, with spiral thickening, perforations simple, intervascular pitting alternate, members moderately to extremely short. **Parenchyma** absent. **Rays** typically wide (6–12 cells), high and with few or no uniseriata, homogeneous or almost so. **Fibres** with small simple pits, sometimes with occasional septa and sometimes storied, moderately to extremely short.

LEAF

Usually dorsiventral. **Hairs** infrequent, mostly unicellular or uniseriate. Glandular hairs with a uniseriate stalk and ellipsoidal head occur in *Epimedium*. **Brown dots**, resembling lenticels, recorded on the lower surface in *Berberis feddeana* Schn., but similar bodies said not to be consistently present in other species of *Berberis*. Lower **epidermis** papillose in certain species of *Berberis*, *Epimedium*, *Jeffersonia*, and *Mahonia*. **Stomata** generally confined to the lower surface; ranunculaceous. Sclerenchyma sometimes present below the upper epidermis in *Berberis* and *Mahonia* spp. Grooves present in the lower surface of *Berberis empetrifolia* Lam. **Mesophyll** not clearly differentiated into palisade and spongy portions in *Epimedium* according to Solereder, and in *Hydrastis* according to Maue (1460). **Midrib** with a varying number of vascular bundles, often collectively surrounded by a sclerenchymatous sheath, especially in the Berberidoideae. According to Solereder the number of bundles in the principal veins has taxonomic value as follows. One bundle in *Caulophyllum*, *Jeffersonia*, and *Leontice*; several in *Achlys*, *Berberis*, *Diphylleia*, *Epimedium*, *Hydrastis*, *Mahonia*, *Nandina*, and *Podophyllum*. This is of doubtful value, however, because it is also stated by Holm (1017) that in *Jeffersonia* there are 2 bundles in the main veins. **Petiole**. Widely spaced vascular bundles recorded in *Epimedium*, *Podophyllum*, and *Vancouveria*. An arc of a few petiolar vascular strands noted at Kew in transverse sections through the distal end in a few species of *Berberis*; a circle of bundles in the corresponding region in *Epimedium* and *Podophyllum*, but with additional medullary bundles in the last of these genera; an adaxially flattened ring of bundles noted in *Mahonia aquifolium* Nutt. Wide **secretory canals** recorded in the phloem of *Caulophyllum thalictroides* (L.) Michx. by Holm (1016). Yellowish or greenish prismatic **crystals** (Fig. 15 A–B) of an organic substance of unknown composition recorded in the upper epidermal cells of certain species of *Mahonia*.

It has been claimed by Maue (1460) that the leaves of the genera *Berberis*, *Epimedium*, *Hydrastis*, and *Mahonia* can be distinguished from one another by the following characters. *Berberis* by the polygonal cells of the upper epidermis, oval unligified stomata, and the absence of hairs; *Epimedium* by the possession of multicellular hairs; *Hydrastis* by the fact that the spongy and palisade regions of the mesophyll are not distinct, and by the presence of unicellular, ligified hairs on both surfaces; *Mahonia* by sinuous anticlinal walls to the cells of the upper epidermis, rounded, ligified stomata and the absence of trichomes; *Podophyllum* by the presence of calcium oxalate crystals in the mesophyll, and a single layer of palisade tissue.

AXIS

YOUNG STEM (Fig. 17 A, B, and E)

Cork arising in the outer part of the pericycle in some species of *Berberis*, but more superficial in others; sub-epidermal in *Podophyllum*. Cork cells usually comparatively thin-walled and with wide lumina. **Pericycle** generally

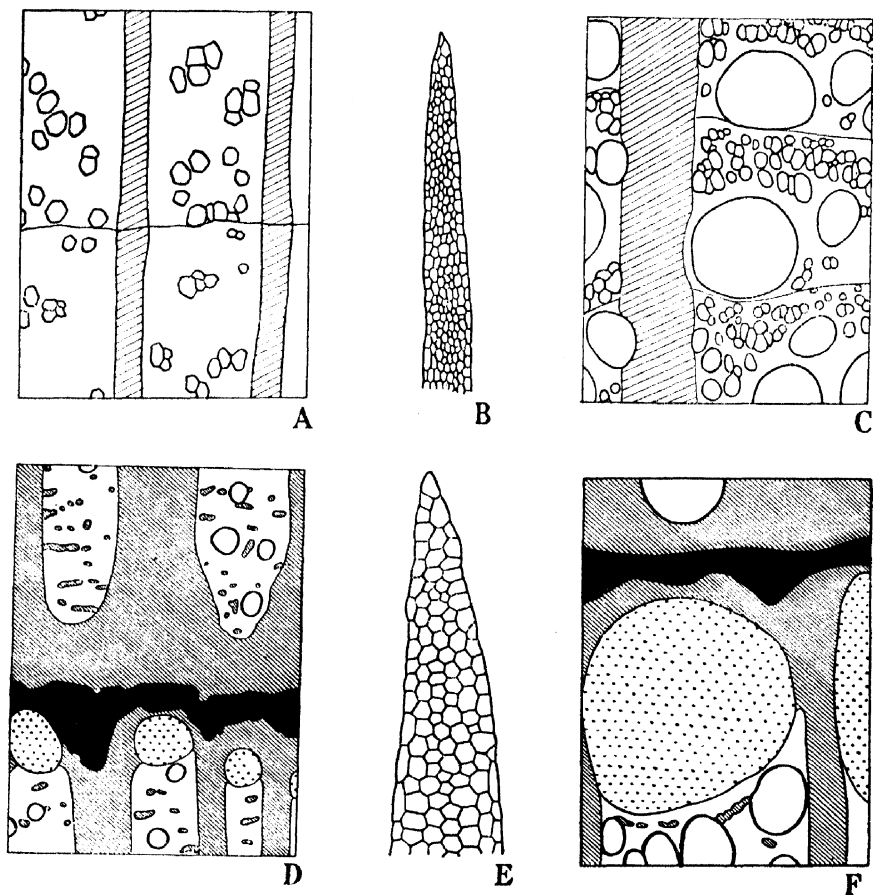


FIG. 16. BERBERIDACEAE, A-B and E; LARDIZABALACEAE, C; MENISPERMACEAE, D and F

A, *Berberis darwinii* Hk. T.S. B, *B. aristata* DC. Ray. C, *Akebia quinata* Decne. T.S. D, *Abuta concolor* Poepp. et Endl. T.S. E, *Berberis tenuifolium* Lindl. Ray. F, *Tiliacora glycosmantha* Diels. T.S.

including a continuous ring of fibres in *Berberis* according to Harvey-Gibson and Horseman (916), but observations at Kew suggest arcs of fibres external to the phloem strands to be more common. The stem of *Berberis aristata* DC. is stated by Short (2095) to be distinguishable from that of allied species of *Berberis* by the presence of large crescents of pericyclic fibres adjoining each phloem strand. **Vascular bundles** separated by broad primary rays in *Berberis*, and *Mahonia*. Transverse sections of aerial stems exhibiting widely spaced and generally scattered bundles in herbaceous and semi-herbaceous

genera such as *Achlys*, *Diphylleia*, *Epimedium*, *Hydrastis*, *Jeffersonia*, *Leontice*, *Podophyllum*, and *Vancouveria*. Vessels mostly with simple perforations; scalariform plates also occur in *Berberis*. **Phloem** with sieve plates on the bevelled ends of the sieve tubes, and sometimes on the lateral walls as well. Peripheral part of the **pith** of the woody genera consisting of cells with thicker walls than those at the centre.

WOOD (Fig. 16 A-B and E)

Vessels very small (25–50 μ mean tangential diameter), the late-wood vessels of *Berberis* sometimes little wider than the fibres and angular in cross-section; commonly in irregular clusters (Fig. 16 A), which tend to be grouped in ulmiform bands in *Berberis*, e.g. in *B. aquifolium* Linn., and in radial lines, in at least the early rings, in *Mahonia tenuifolium* (Lindl.) Britton, and in radial lines of almost solitary vessels in *Nandina domestica* Thunb.; seldom touching the rays; 25–50 per sq. mm.; ring-porous in some species of *Berberis*, e.g. *B. aristata* DC. and *B. vulgaris* Linn., and semi-ring-porous in some other species of *Berberis* and in *Nandina*; with spiral thickening. Perforations typically simple, slightly oblique; scalariform plates with very few bars reported by Solereder to be occasionally present in *Berberis*; Tupper (2295) refers to exclusively scalariform plates in *Berberis*. Imperfect vessel members frequent; these may be the spirally thickened 'tracheids' of *Nandina*, to which Solereder refers. Intervascular pitting alternate, moderate-sized. Pits to ray cells very rare, similar to the intervacular pitting. Mean member length 0.15–0.27 mm. **Parenchyma** absent. **Rays** typically high and wide; usually up to 6–12 cells wide, but up to 25 cells wide in *B. kavakana* Hay (1206); commonly more than 2 mm. and sometimes more than 5 mm. high, the tall rays often showing evidence of subdivision into smaller units; uniseriatae very few or lacking; about 3 rays per mm.; homogeneous (Kribs's Type II) or with only a slight difference between marginal and central cells in *Berberis*, though with moderately distinct sheath cells in *B. darwinii* Hook. (Fig. 16 B); composed entirely of small square cells in *Mahonia tenuifolium*; with numerous crystals in *Mahonia*. **Fibres** with moderately numerous, small, simple pits on the radial and tangential walls. Occasionally septate in *Berberis* and *Nandina*. Walls thin to moderately thick. Sometimes storied in *Berberis* and *Mahonia*. Mean length 0.3–0.75 mm.

RHIZOME

A single ring of **vascular bundles** commonly present in *Achlys*, *Caulophyllum*, *Diphylleia*, *Epimedium*, *Hydrastis*, *Jeffersonia*, and *Podophyllum*, but in all of these genera the bundles are sometimes in two rings or scattered. Additional **cortical bundles**, consisting mainly of sclerenchyma, present in species of *Achlys*, *Diphylleia*, and *Podophyllum*. Xylem of *Vancouveria hexandra* C. Morr. et Dec. embedded in a ring of sclerenchyma except in parts of old specimens, according to Harvey-Gibson and Horseman (916). **Pericycle** generally devoid of fibres in herbaceous forms (except *Epimedium*), and *Leontice altaica* Pall. Two zones of pericyclic fibres recorded in *Epimedium*, *Nandina*, and a few species of *Mahonia*.

The microscopical features of commercial *Podophyllum* rhizome are described under 'Economic Uses'.

ROOT

Very little secondary thickening in the roots of *Podophyllum*. **Endodermis** well defined in this genus. **Mycorrhiza** recorded in the thin roots of *Caulophyllum thalictroides* (L.) Michx. and '*Jeffersonia diphylla* (L.) Pers.'

TAXONOMIC NOTES

The stems of the woody genera *Berberis* and *Mahonia* are, at first sight, very dissimilar in structure from the aerial stems of herbaceous genera such as *Podophyllum*. It is quite possible that these differences are partly associated with the diverse mechanical requirements of herbaceous and woody plants respectively, although, from the taxonomic standpoint, it seems probable that, if the herbaceous and woody genera have had a common ancestor, it must have been somewhat remote from the present-day representatives of the family. Himmelbaur (976), on the other hand, has expressed the view that the stem anatomy of the Berberidaceae is such as to suggest that all the members of the family have been derived from one type. The similarity of the herbaceous genera with scattered bundles to certain of the Ranunculaceae and hence to the Monocotyledons has already been described under Ranunculaceae. Harvey-Gibson and Horseman (916), however, take exception to Solereder's statement that the stem structure of *Jeffersonia* is Monocotyledonous. The stem structure of *Berberis* and *Mahonia* is rather suggestive of that of the Menispermaceae. The presence of berberin in the Menispermaceae and Berberidaceae is also noteworthy in this connexion.

The anatomy of the wood of the shrubby genera indicates a moderately high level of specialization, particularly the very short vessel members, the homogeneous rays and the libriform fibres, which are sometimes storied.

ECONOMIC USES

The fruits of numerous species of *Berberis* and *Mahonia* are edible, whilst the roots of *Berberis* spp. are used for medicinal purposes. A dye is extracted from the yellow bark and roots of *Berberis* spp. The dried rhizomes of *Podophyllum peltatum* Linn. and *P. hexandrum* Royle from North America and India, respectively, are of medicinal value because they contain podophyllin. Microscopical features of the rhizome of *P. peltatum* include the following. Epidermis of axially elongated cells filled with reddish-brown, tanniferous contents. Cork arising in the hypoderm, consisting of 2 or 3 layers of cells. One or two layers of large, somewhat collenchymatous, empty cells present beneath the cork. Cortex and pith parenchymatous, most of the cells containing simple or compound starch grains. Isolated cluster crystals scattered throughout the parenchymatous tissues. A few of the parenchymatous cells filled with a yellow secretion. Endodermis not distinct in the rhizome, although well defined in the root. Pericycle, in some instances, marked by small strands of fibres situated externally to the vascular bundles. (In at least one sample in the Kew Museums these fibres were very infrequent.) Vascular system consisting of a circle of 20 to 30 collateral vascular bundles, separated from one another by broad rays. Many of the xylem vessels filled with yellow contents. Groups of sclerenchymatous cells sometimes present on the inside of the vascular bundles.

The rhizome of the Indian drug *Podophyllum hexandrum* Royle (syn. *P. emodi* Wall.), which also occurs in commerce, is generally distinguishable from *P. peltatum*, according to Wallis and Goldberg (2350, 2351), by the following characters. (i) Absence of epidermal cells with brown contents. (ii) The smaller size of the cluster crystals. (iii) The almost complete absence of pericyclic fibres. (This last character appears to be somewhat unreliable, as samples occur in the Kew Museums in which pericyclic fibres were more numerous in the Indian than in the American species. A more reliable method of distinguishing the rhizome of the 2 species in question is by grinding up the rhizome with 90 per cent. alcohol, filtering, and adding a few drops of a copper acetate solution. This treatment gives a green coloration with the American drug and a brownish-yellow one with the Indian. This mode of distinction seems to be effective even with material stored for 50 years in a museum.)

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Achlys, Berberis,* Caulophyllum,* Diphyllia, Epimedium,* Hydrastis, Jeffersonia, Leontice, Mahonia,* Nandina, Podophyllum,* Vancouveria.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Berberis, Mahonia, (Nandina).

LITERATURE

(i) On General Anatomy

Blaque and Maheu 205, Ewert 667, Harvey-Gibson and Horseman 916, Himmel 975, Himmelbaur 976, Holm 1016, 1017, 1021, 1063, Kumazawa 1298, Maue 1460, Short 2095, Stearn 2189, Wallis and Goldberg 2350, 2351, Worsdell 2469.

(ii) On Wood Structure

Dadswell and Record 533, Howard 1088, Kanehira 1206, 1209, Record 1843, 1851, Record and Hess 1886, Tupper 2295, Yamabayashi 2478.

19. CIRCAEASTERACEAE

This family is represented by the single species *Circaeaster agrestis* Maxim. from the Himalayas. The plant is a herb with a basal rosette of leaves. It has not been examined microscopically in recent years, and the following features are taken from Solereder's account.

Cells of the upper **epidermis** of the leaf elongated parallel to the midrib. **Stomata** small, ranunculaceous; confined to the lower surface. Vascular bundles of the **veins** not accompanied by sclerenchyma. Vascular system of the stem, like that of the main root, consisting of a diarch xylem plate with only a small amount of secondary wood and phloem produced on both sides.

The genus was included in the Chloranthaceae in the Bentham and Hooker system, but was placed amongst the Berberidales by Hutchinson. The taxonomic position of the family is very uncertain.

GENUS DESCRIBED

Circaeaster.

20. LARDIZABALACEAE

(FIG. 16 on p. 60; FIG. 17 on p. 65)

SUMMARY

A small family consisting mostly of lianes, but including some erect shrubs. It is confined to Eastern Asia and temperate South America. The most constant anatomical characters are the widely spaced **vascular bundles** of the axis, usually separated by broad, generally lignified primary medullary rays; the circle of separate bundles, visible in transverse sections through the distal end of the **petiole**; the frequent occurrence of solitary **crystals** in the pericyclic fibres of the axis or in the parenchymatous cortical cells immediately adjacent. The outer part, or, in some instances, the whole of the **pith**, consists of thick-walled, pitted parenchyma.

The wood exhibits the following features. **Vessels** large, sometimes with spiral thickening, perforations wholly simple or with a few scalariform plates, intervacular pitting alternate, members of medium length to very short. **Parenchyma** very sparse or absent. With broad primary **rays** only. **Fibres** with simple pits, sometimes septate and storied, extremely short in *Akebia*.

LEAF

Dorsiventral. **Epidermis** on both surfaces consisting of cells with sinuous anticlinal walls, especially on the lower side; strongly papillose on the lower surface in all examined species except *Holboellia coriacea* Diels. A well-developed **hypoderm** present in *Holboellia* but not observed in the other genera. **Stomata** confined to the lower surface; ranunculaceous. **Mesophyll** including several layers of palisade cells. **Veins** embedded in the mesophyll, often tending to be vertically transcurrent by sclerenchymatous elements. **Petiole** (Fig. 17 C and D), in transverse sections through the distal end, exhibiting, e.g. in *Decaisnea fargesii* Franch., a ring of individually distinct vascular bundles, each accompanied on the outside by a well-developed strand of fibres, the latter usually with wide lumina; similar, but with fibres forming a continuous ring, e.g. in *Akebia lobata* Decne. Solitary **crystals** present in the cells immediately external to the pericyclic fibres in *Akebia*, but much more numerous in *A. quinata* Decne. than in *A. lobata* Decne.; observed also in the sub-epidermis in the first of these species. No crystals around the vascular bundles of the veins observed in *Holboellia coriacea*.

AXIS

YOUNG STEM (Fig. 17 F)

Cork arising superficially. **Pericycle** including well-defined strands of fibres outside the phloem groups. **Vascular system** invariably consisting of widely spaced bundles, separated by conspicuous, generally lignified rays. **Phloem** masses well developed but containing no sclerenchyma. **Xylem** including vessels of wide diameter; perforations generally simple, but only scalariform plates observed at Kew in *Decaisnea fargesii* Franch. (See also

'Wood'.) Outer part of the **pith** composed of strongly lignified, pitted cells in *Akebia* and *Holboellia*, the centre being occupied by thin-walled cells; the whole tissue composed of lignified cells in *Stauntonia hexaphylla* Decne.

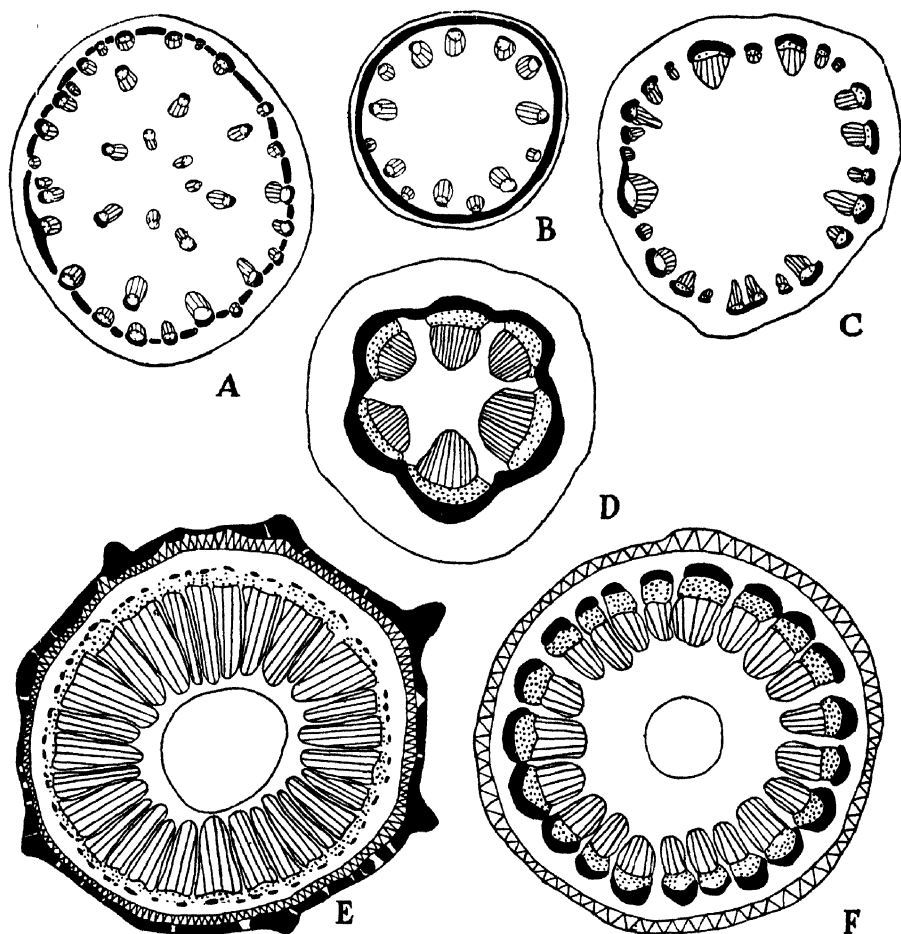


FIG. 17. BERBERIDACEAE, A-B and E; LARDIZABALACEAE, C-D and F

A, *Podophyllum peltatum* Linn. S.em $\times 8$. B, *Epimedium alpinum* Linn. Aerial stem $\times 15$. C, *Decaisnea fargesii* Franch. Petiole $\times 13$. D, *Akebia lobata* Decne. Petiole $\times 60$. E, *Berberis thunbergii* DC. Stem $\times 15$. F, *Akebia lobata* Decne. Stem $\times 30$.

Solitary **crystals** abundant in the pericyclic fibres and pith of *Holboellia coriacea* Diels; similar crystals, mostly situated in cells immediately external to the pericyclic fibres, noted in *Akebia* and *Lardizabala*. Clustered crystals observed only in the central part of the pith of *Holboellia coriacea*.

WOOD (Fig. 16 c)

Vessels of two distinct sizes in *Akebia quinata* Decne. very large and solitary or very small and in tangential multiples and clusters (Fig. 16 c); Solereder refers to spiral thickening in the smaller vessels of *Holboellia* and

Lardizabala bitermata Ruiz. et Pav. Perforations simple, except for a few scalariform plates with few bars in *Holboellia* (2158). (See, however, under 'Young Stem'.) Intervascular pitting alternate, large; pits to ray cells sometimes large and simple. Storied in *Akebia quinata*. Mean length about 0.23-0.55 mm., shortest in *Akebia*. **Parenchyma** very sparse or absent. **Rays** limited to broad and high primary rays, which are unligified and, according to Solereder, do not become closed by interfascicular wood, but form longitudinal plates that split up the wood into segments. **Fibres** with large bordered pits in *Akebia* and *Lardizabala* (2158), but with simple pits in *Holboellia*; with fine septa and storied in *Akebia quinata*. Mean length about 0.4 mm. in *Akebia*.

TAXONOMIC NOTES

This small family is closely related to the Berberidaceae in which it was included by Bentham and Hooker. It has also been suggested by Harvey-Gibson and Horseman (916) that it is in some respects intermediate between the Berberidaceae and Menispermaceae. The widely spaced vascular bundles and general appearance of the stems are very alike in all 3 families. The resemblance to the woody Ranunculaceae, such as *Clematis*, and some of the Aristolochiaceae are also noteworthy, although it should be remembered that these similarities may be partly bound up with the climbing habit of the plants. *Sargentodoxa*, which differs somewhat from the Lardizabalaceae, is here treated as the sole genus in a distinct family.

ECONOMIC USES

The fruits of *Akebia lobata* Decne. are eaten in Japan, and the sliced stems of *A. quinata* Decne. used medicinally in China.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Apart from a few scattered statements in the literature, the above description was based mainly on fresh material of the following species grown at Kew: *Akebia lobata* Decne.,* *A. quinata* Decne.,* *Decaisnea fargesii* Franch.,* *Holboellia coriacea* Diels,* *Stauntonia hexaphylla* Decne.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Akebia, (*Holboellia*), *Lardizabala*.

LITERATURE

(i) On General Anatomy

Bowman 250, Harvey-Gibson and Horseman 916.

(ii) On Wood Structure

Garratt 747, Record 1851.

21. SARGENTODOXACEAE

SUMMARY

Sargentodoxa cuneata Rehd. et Wils., originally named *Holboellia cuneata* Oliv. and included in the Lardizabalaceae, was given the status of a distinct family by Stapf (2186). The species occurs in Central China. According to Lemesle (1355) the anatomy of the stem was described by Réaumbourg, and the following description is based mainly on the last author's account, as summarized and amplified by Lemesle.

AXIS

STEM

Epidermis composed of quadrangular cells, but rounded on the outer surface; outer wall thick and cutinized. Primary **cortex** consisting of about 12 layers of flattened cells. **Pericycle** completely sclerosed, forming a broad, sinuous ring. **Cork** arising in the innermost layer of the pericycle. **Vascular system** consisting of 4 large, distinct bundles alternating with smaller ones. (According to Solereder the large bundles constitute an inner ring.) **Xylem**. Vessels up to 200 μ in diameter. Ground tissue of the xylem consisting of radial rows of fibres having circular bordered pits with obliquely crossed apertures in both the radial and tangential walls. (Lemesle calls these fibres 'tracheides à ponctuations aréolées'.) **Pith** parenchymatous, but including a group of sclerosed cells at the centre. Large **secretory cells** with tanniniferous contents reported by Solereder to occur in association with the vascular bundles.

TAXONOMIC AND PHYLOGENETIC NOTES

In Lemesle's opinion, the floral characters and the nature of the fibres which constitute the ground tissue of the xylem indicate that *Sargentodoxa* is a very primitive angiosperm. Comparisons, on rather slender evidence, are even made with the Cycadaceae and Bennettitales. *Sargentodoxa* is clearly differentiated from the Lardizabalaceae by its deep-seated cork.

GENUS EXAMINED

Sargentodoxa.

LITERATURE

On General Anatomy

Henderson 952, Lemesle 1355, Stapf 2186.

22. NYMPHAEACEAE

(Fig. 18 on p. 68; Fig. 19 on p. 72)

SUMMARY

Aquatic herbs which include the familiar water-lilies. The family occurs in Tropical and North Temperate regions. Its members possess closed, scattered **vascular bundles** resembling those of the Monocotyledons. As in most aquatic herbs there are numerous **intercellular spaces** in the parenchymatous tissues. **Air passages** arise in the position of the primary xylem owing to the breakdown of the latter. True vessels are absent. Branched sclerenchymatous

idioblasts (Fig. 18 A) are common. **Hairs** uniseriate, of several cells, some secreting mucilage. Calcium oxalate frequently deposited on the cell walls. Clustered **crystals** occur in the stem and leaf of *Nelumbium* and rhombic crystals of brasenin recorded in *Brasenia*. Articulated **laticiferous tubes** or **sacs**, with thin suberized walls, are present in the parenchymatous tissue of all organs, as well as in the vascular bundles; those of *Nuphar* are nearly isodiametric, generally solitary or 2-3 in a linear row, but those occur-

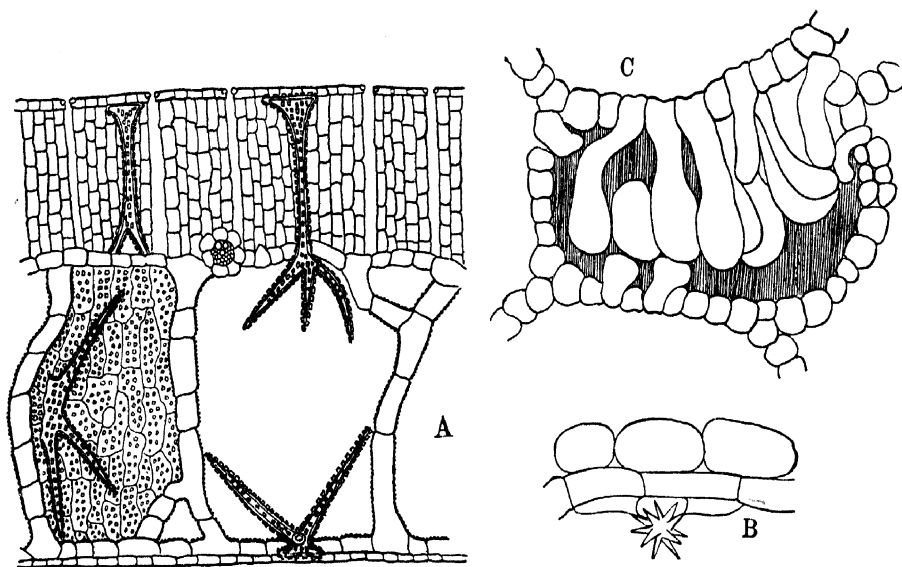


FIG. 18. NYMPHAEACEAE

A, Transverse section through the leaf of *Nymphaea marliacii* Hort.; the crystals in the walls of the idioblasts and of the spongy parenchyma are drawn larger than they are in reality. B, Transverse section through the wall of an air passage from the petiole of *Nelumbium speciosum* Willd., with a cell bearing a clustered crystal. C, Intercellular space of *Brasenia peltata* Pursh., filled with mucilage hairs. A-B, by Solereder, C, after Schrenk.

ring in the bundles are more elongated. The laticiferous sacs are arranged together in long rows in *Brasenia* and *Cabomba*; those of *Euryale*, *Nymphaea*, and *Victoria* tubular and of considerable length, although consisting of only a few cells. **Rhizomes** and **stolons** are often polystelic. **Root hairs** arise from specialized cells. This feature is common amongst the Monocotyledons but rare amongst the Dicotyledons. For a detailed description of the anatomy of *Nymphaea* Conard's (457) monograph should be consulted.

LEAF (Fig. 18 A-C and Fig. 19 C-E)

Dorsiventral, with abundant intercellular spaces in the spongy tissue. **Hairs** uniseriate; generally confined to young organs, becoming detached from older ones. Hairs consisting of clothing and mucilaginous kinds. Clothing hairs frequently uniseriate with 2-3 basal cells, the latter being much shorter than the remainder and provided with suberized lateral walls. Mucilage hairs shorter than the clothing hairs, but provided with an enlarged terminal cell. **Stomata** ranunculaceous; generally confined to the upper surface; closed by the interlocking of the cuticular ridges of the guard cells

in *Euryale*, *Nuphar*, *Nymphaea*, and *Victoria*. Floating leaves of *Nymphaea alba* Linn. with stomata evenly distributed over the greater part of the upper surface of the leaf lamina, but absent from the region of attachment of the petiole to the lamina. Stomata, in the region immediately surrounding that from which they are absent, provided with guard cells twice as large as those elsewhere. Large stomata less numerous than small ones. Average number per sq. mm. under normal light intensity 460, maximum recorded 524, minimum 150. Submerged leaves, although apparently similar in external appearance, are of two kinds, with and without stomata respectively. Stomatal distribution in terrestrial forms similar to that of submerged plants. Stomatal frequency is reduced by intense illumination according to Roshardt (1956, 1957). In *Nuphar luteum* Sibth., Grüss (830, 831) found stomata to be absent from or infrequent in aerial leaves, those on the lower surface being confined to the regions above the marginal bundles. **Hydathodes** present in the centre of the upper surface in *Nelumbium speciosum* Willd., and at the points of junction of the anastomosing veins of '*Brasenia peltata* Pursh'. **Haustoria**, believed to serve for the uptake of water and dissolved mineral substances, present in *Nuphar luteum*, *Nymphaea lotus* Linn. and *Victoria regia* Lindl.; those of *Nuphar luteum* consisting of 2 small basal cells with lignified walls, bounded externally by a swollen one extending to the exterior of the leaf; a large swollen cell present internally to the 2 lignified basal ones. Haustoria of *Nymphaea lotus* and *Victoria regia* similar but differing in details. About 200 haustoria per sq. mm. present in floating and 9-112 per sq. mm. in aerial leaves of *Nuphar luteum* according to Grüss. Branched sclerenchymatous **idioblasts** (Fig. 18 A) varying in shape within a single species, and which may be stellate, girder- or H-shaped, recorded by Solereder in *Euryale*, *Nuphar*, *Nymphaea*, and *Victoria*; sometimes covered with minute crystals of calcium oxalate. Idioblasts stated to be absent from *Brasenia*, *Cabomba*, *Nelumbium*. Walls of the idioblasts of *Nuphar* and *Nymphaea* pitted where in contact with adjacent cells. **Spines**, containing vascular tissue, present in *Euryale*. **Transparent dots** of unknown physiological significance, but believed to consist of pits formed by the death of the tissues in the regions where present, occur in the leaves of *Victoria*. The pits in old leaves become filled with algae or deposits of lime. **Fat** frequent in guard and mesophyll cells of *Nuphar luteum*, becoming converted to starch under inadequate illumination. **Petiole**, in transverse sections, exhibiting normally orientated, double bundles in *Brasenia* and *Cabomba*; with mixed simple and double, but normally orientated bundles in *Euryale*, *Nymphaea*, and *Victoria*; with mixed normal and inversely orientated bundles in *Nelumbium*. For **diaphragms** in the petiole see under 'Axis'.

Enlarged mucilaginous cells (Fig. 18 c) sometimes project into the intercellular air spaces, e.g. in *Brasenia*. Clustered **crystals** (Fig. 18 B) recorded by Solereder in certain small cells in the partitions between the air lacunae in the petiole (and stem) of *Nelumbium*, the crystalliferous cells projecting into the intercellular cavities.

The structure and distribution of the vascular bundles and air canals in the petioles and peduncles of different species of *Nymphaea* are of considerable interest, and should be useful in identifying species. For details see the plate on p. 59 of Conard's (457) monograph.

AXIS

With abundant **intercellular spaces** of schizogenous origin, arranged in circles in *Euryale*, *Nymphaea*, and *Victoria*, but distribution reticulate in *Nuphar*. **Diaphragms** traverse the intercellular spaces in *Nuphar luteum* Sibth., *Nymphaea alba* Linn., *N. lotus* Linn., and *Victoria regia* Lindl., but are not universally present in all the organs of these species; absent from the petiole and peduncle of *Nymphaea*, although present in the corresponding regions of *Victoria regia*. Diaphragms of *Nymphaea alba* and *Victoria regia* found by de Bruyne (300) to be very delicate, consisting of a single layer of elongated cells united by lateral prolongations; those in the petiole and peduncle of *Nuphar luteum* consisting of a kind of spongy tissue occupying the whole lumen of the canal. **Vascular bundles** in transverse sections, like those of the Monocotyledons, appearing irregularly distributed, without cambium or true vessels, but provided with long tracheids possessing spiral or annular thickenings. Primary xylem becoming disorganized, and thus giving rise to schizogenous cavities, each bundle then consisting of a canal and a phloem strand. Sclerenchyma absent from the bundles. **Peduncle** of *Brasenia* and *Cabomba* with 3 simple, normally orientated bundles arranged in a triangle; simple and double, but normally orientated bundles occur in the peduncle of *Euryale*, *Nymphaea*, and *Victoria*; normal and inversely orientated bundles in the corresponding position in *Nelumbium*. *Barclaya* and *Nuphar* possess simple bundles throughout.

RHIZOME

Frequently containing a confused mass of bundles. Polystelic in certain species including *Victoria regia* Lindl., where each stele consists of a ring of about 20 bundles. Bundles in the stolons of *Nymphaea mexicana* Zucc. (syn. *Castalia flava* Leitn.) arranged in 4 or 5 widely separated groups of steles, each enclosed in an endodermis and surrounding a protoxylem group. Two steles, each consisting of a pair of bundles, observed by Arber (29) in the stolons of *Cabomba*. Rhizomes almost universally astelic according to Van Tieghem and Schoute as cited by Solereder, *Nelumbium* alone possessing a general endodermis around the central cylinder. Rhizomes stated in the literature to have double bundles in *Brasenia* and *Cabomba*; simple, normally orientated bundles in *Euryale*, *Nymphaea*, and *Victoria*; mixed bundles exhibiting normal and inverse orientation respectively in *Nelumbium*.

ROOTS

With numerous **diaphragms** in *Nuphar luteum* Sibth., *Nymphaea alba* Linn., *N. lotus* Linn., and *Victoria regia* Lindl.; those of *Nuphar luteum* said by de Bruyne (300) to be composed of a number of cells loosely attached to the walls of the canals, thus giving the appearance of a membrane with holes at the margins as seen in transverse sections. **Root hairs** arising from specialized cells, as in many Monocotyledons.

TAXONOMIC NOTES

The most interesting features are the closed scattered bundles of the type characteristic of the Monocotyledons, the absence of vessels from the xylem,

and the occurrence of polystely. The absence of sclerenchyma and the presence of abundant intercellular spaces are characters which are probably correlated with the aquatic habitat of the family, and possess but little taxonomic significance.

ECONOMIC USES

The Water Lilies are cultivated as decorative plants. Arber (29) has recorded that the long peduncles of Water Lily flowers are sold in bazaars at Cairo as tobacco pipes.

GENERA DESCRIBED

Barclaya, Brasenia, Cabomba, Castalia, Euryale, Nelumbium, Nuphar,* Nymphaea,* Victoria.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Arber 29, de Bruyne 300, Conard 457, Green and Buck 808, Grüss 830, 831, Gwynne-Vaughan 853, Roshardt 1956, 1957.

23. SARRACENIACEAE

(FIG. 19 on p. 72)

SUMMARY

An American family of herbs with rhizomes bearing a rosette of radical, tubular leaves, the latter provided with specialized glands and hairs which serve for entrapping insects and other small organisms which are subsequently digested by the plant as food.

LEAF (Fig. 19 A-B)

Distal portion tubular, with a petiolar region below. Upper part of petiole expanded on one side as a laminar 'wing'. External **epidermis** provided with **secretory glands**, accompanied in some species by upwardly directed hairs. Glands especially numerous on the laminar wings in *Heliamphora*. Passing from the apex downwards several distinct zones may be recognized on the inside of the leaf. (1) **Glandular zone** occupying the inner surface of the lid of *Heliamphora* and *Sarracenia*, and of the hood of *Darlingtonia*. Glands, stomata (not accompanied by subsidiary cells) and downwardly directed hairs present in this region, the glands of *Heliamphora* being of 2 distinct sizes. (2) **Slippery zone**, consisting of epidermal cells with downwardly directed projections, overlapping like fish scales. Glands sometimes present, but stomata and hairs absent. (3) **Eel-trap zone** occupying the greater part of the tube, with long, downwardly directed, needle-shaped hairs, and numerous glands, but no stomata. The extreme basal portion of the leaf is provided with a smooth surface. (Glands absent from the inside of the leaf of *Darlingtonia* except for the hood according to Solereder.) [Solereder also states that in *Heliamphora* the slippery zone is lacking, and the stomata in the eel-trap zone are elevated. This is not in agreement with Macfarlane's (1409) description in which it is stated that in *Heliamphora* there is a smooth region below

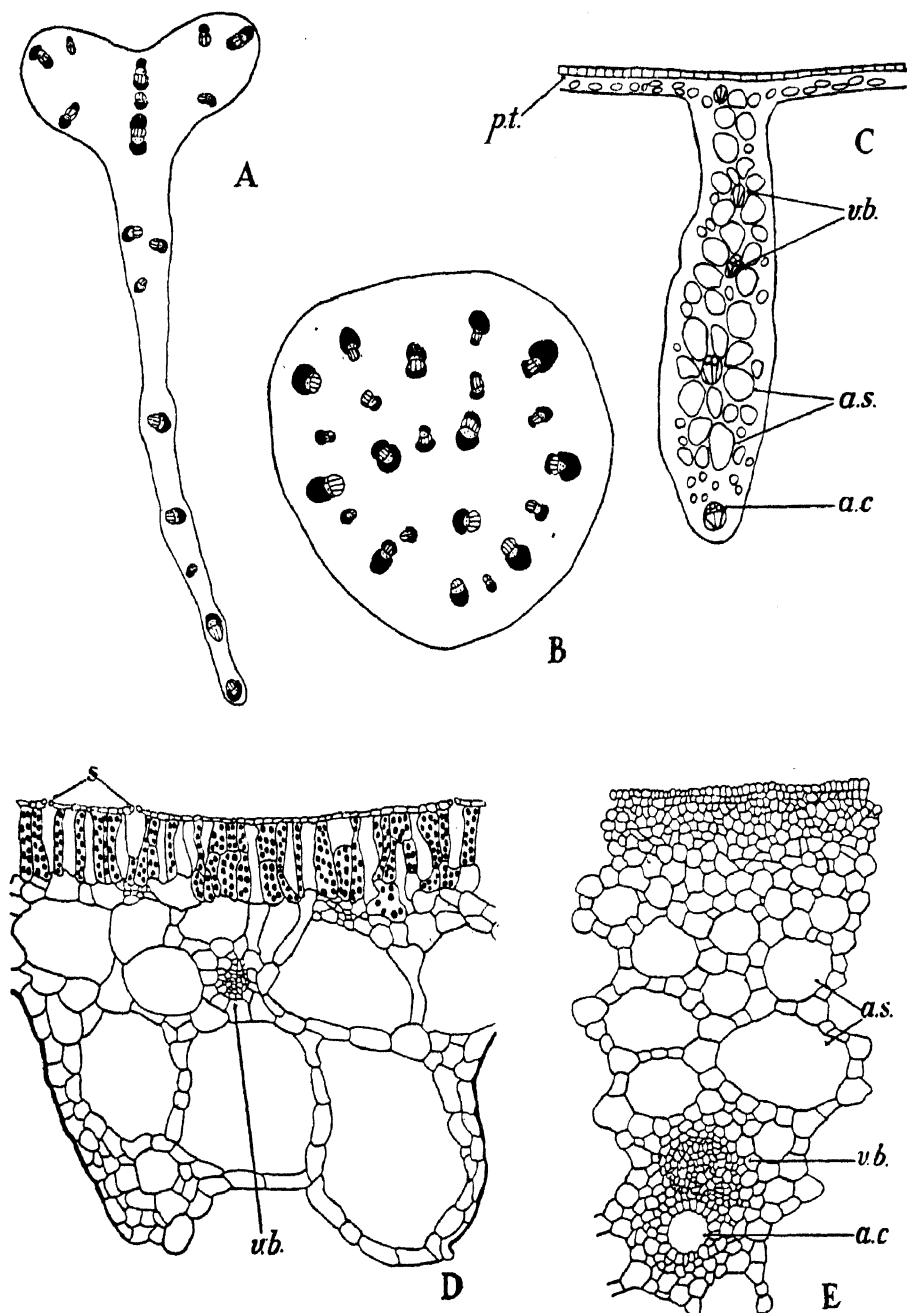


FIG. 19. *SARRACENIACEAE*, A-B; *NYMPHAEACEAE*, C-E

A, *Sarracenia purpurea* Linn. Petiole, through wing, $\times 9$. B, *S. purpurea* Linn. Base of petiole $\times 15$. C, *Victoria regia* Lindl. Lamina $\times 15$. D, *V. regia* Lindl. Lamina $\times 50$. E, *Nuphar luteum* (L.) Sm. Outer part of petiole $\times 50$.
a.c. Air canals. a.s. Air spaces. pt. Palisade tissue. vb. Vascular bundle.

Fig. C shows the lamina with a rib projecting from the lower surface. In Fig. D only the upper part of one of the ribs is shown.

the glandular, hairy inner surface of the lid, whilst at the base of the tube there are a few thickened hairs. There appear to be considerable variations in different species of all the genera.]

Modified circular areas, in which the epidermis of the outer is separated from that of the inner surface only by specially thin portions of the mesophyll, occur in the upper part of the pitchers of *Sarracenia drummondii* Croom, *S. minor* Walt., and *S. psittacina* Michx. Each of these areas is surrounded by a fence of hairs. **Scale or autumnal leaves** of *Sarracenia* spp. bear numerous glands on both upper and lower surfaces. Stomata absent from the upper epidermis in all species, but infrequently on the lower (outer) epidermis in *S. purpurea* Linn. The anatomical facts suggest that the scale leaves are reduced pitchers. **Petiole**, in transverse sections, exhibiting an irregular crescent of collateral vascular bundles, each bounded internally and externally by sclerenchyma but embedded in loose, starch-containing tissue, the starch grains being far more numerous in some of the cells than in others. According to Macfarlane the bundles in the cylindrical portion of the petiole are arranged in a discontinuous circle, bounded externally by a cortex of cells containing chlorophyll. Other irregularly distributed vascular strands also occur within the circle just mentioned. In the section of the petiole of *S. purpurea* used in the preparation of Fig. 19 B the demarcation between the outer ring of bundles and the scattered ones towards the centre is not very clear. Two sets of bundles present in the laminar wing with their xylem groups inwardly directed (Fig. 19 A).

RHIZOME

Epidermis with brown pigment in the cell cavities; bounded internally by 2-3 layers of **hypoderm**, the outer cells being lignified. **Cortex** broad. **Vascular bundles** collateral, of varying size and shape, arranged in a discontinuous ring and separated by rays of unequal width. Ring of bundles more nearly closed in *Darlingtonia* than in *Sarracenia*. Bundles bounded internally and externally by sclerenchyma. **Xylem** containing a few vessels with spiral thickening, and more numerous vessels with scalariform perforation plates.

ROOT

Primary structure pentarch or hexarch. Schweiger (2063) has recorded the following information concerning a root of *Sarracenia chelsoni* Hort. 1 mm. thick. Surface bounded by a 3-layered **hypodermis** with thickened walls and brown contents. **Cortex** spongy, with abundant intercellular spaces, bounded internally by an **endodermis** of small cells with scarcely thickened walls. **Xylem** arranged in 10 large groups. Metaxylem of *S. purpurea* Linn. said to consist of tracheids, food-storing cells, and large vessels with oblique, scalariform 'septa'. Roots of *Darlingtonia* differ only in minor respects.

TAXONOMIC NOTES

The plants are so specialized in structure in correlation with their peculiar mode of life that it is rather difficult, on anatomical grounds, to decide which of the positions to which the family has been assigned in different systems of classification is most likely to be correct. Schweiger (2063), who made careful anatomical comparisons between *Sarracenia* and *Cephalotus* (Cephalotaceae),

decided that such resemblances as exist between these 2 genera are due to similarities in their mode of life and have no taxonomic significance.

GENERA DESCRIBED

Darlingtonia, Heliophora, Sarracenia.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Arber 32, Lloyd 1383, Macfarlane 1409, Russell 1970, Schweiger 2063, Uphof 2315.

24. PAPAVERACEAE

(FIG. 20 on p. 76; FIG. 25 on p. 92)

SUMMARY

(i) GENERAL

Mainly herbs, but certain genera tending to be shrubby (*Dendromecon*), or small trees (*Bocconia*). The family occurs mainly in temperate and subtropical regions of the Northern Hemisphere. The **stem** of most Papaveraceae exhibits, in transverse sections, a single ring of widely spaced vascular bundles, which are nearly always collateral. The **xylem** groups frequently tend to be V-shaped. Several rings of bundles sometimes present in *Papaver*. **Hairs** scanty, uniseriate, biseriate, or multiseriate. Shaggy hairs occasional. Glandular hairs absent. **Stomata** ranunculaceous. **Petiole**, in transverse sections, commonly exhibiting an arc of vascular bundles not accompanied by sclerenchyma. Various coloured latex present, sometimes in articulated **laticiferous tubes**, but elsewhere in cells or sacs, the latter sometimes arranged in longitudinal rows. **Crystals** of calcium oxalate recorded only in *Bocconia frutescens* Linn. but said to be present in the floral leaves of a few other species. Cluster crystals also noted in *Romneya*. **Alkaloids** are common in the family. These include such well-known substances as morphine and codeine. Berberin, which is characteristic of the Berberidaceae, is known to occur in *Argemone mexicana* Linn.

(ii) WOOD

Vessels small and tending to be ulmiform, or medium-sized and without pattern, sometimes ring-porous and with spiral thickening, perforations simple, intervascular pitting alternate, members of medium length. **Parenchyma** vasicentric. **Rays** all multiseriate, up to 5-12 cells wide, high, heterogeneous. **Fibres** with simple pits, very short.

LEAF

Usually dorsiventral. Simple, uniseriate **hairs** recorded in *Chelidonium*, *Glaucium*, *Roemeria*; shaggy hairs in *Bocconia*, *Macleaya*, *Meconella*, *Meconopsis*, *Papaver*, *Platystemon*. **Spines** present in *Argemone mexicana* Linn. Thickenings recorded on the anticlinal walls of the cells of the **epidermis** of *Glaucium corniculatum* (L.) Curtis. Lower surface slightly papillose in *Sanguinaria canadensis* Linn., and with conical papillae on both surfaces in

Dendromecon rigida Benth. Epidermis frequently covered with wax, especially in *Bocconia* and *Macleaya*. **Stomata** present on both surfaces in *Papaver pilosum* Sibth. et Smith., *P. spicatum* Bois., and *Roemeria dodecandra* (Forsk.) Stapf, but generally confined to the lower surface in other genera and species; ranunculaceous. **Hydathodes** occur in groups on the lower surface of the teeth at the margin of the leaf in certain species of *Papaver*. **Mesophyll** generally including 1 to several layers of palisade cells, but not distinctly differentiated into palisade and spongy regions in *Hesperomecon platystemon* Greene (syn. *Platystigma lineare* A. Gray), *Meconella californica* Torr., *M. oregana* Nutt., and *Papaver somniferum* Linn. Palisade tissue recorded on both sides of the leaf in *Eschscholtzia californica* Cham. **Petiole** (Fig. 20 D-E), in transverse sections through the distal end, exhibiting an arc of vascular bundles in *Chelidonium majus* Linn. (Fig. 20 E), *Eschscholtzia californica*, *Macleaya cordata* (Willd.) R. Br. *Romneya trichocalyx* Eastw. (Fig. 20 D), and *Papaver dubium* Linn. Bundles sometimes very close together or almost fused in *Macleaya cordata*. Sclerenchyma generally scanty in or absent from the petiole, but each bundle is surrounded by a massive layer of fibres in *Bocconia frutescens* Linn. **Crystals** of calcium oxalate recorded only in *Bocconia frutescens*, but clustered crystals observed at Kew in the stem of *Romneya*.

LATEX CANALS AND CELLS

Latex generally present throughout the plant in either (i) articulated **laticiferous tubes**, frequently having sieve plates on the transverse or lateral walls, or (ii) **laticiferous sacs** consisting of more or less elongated cells, either solitary or arranged in longitudinal rows. (According to Solereder, the nature of the latex-containing elements is of diagnostic value in separating certain genera. While this may be true in certain instances, it has also been shown by Holm (1927) that the nature of the laticiferous elements varies in different parts of individual plants of *Sanguinaria canadensis* Linn.). Articulated laticiferous tubes recorded in *Argemone*, *Chelidonium*, *Papaver*, *Roemeria*, and the stem of *Sanguinaria canadensis*, and probably occurring also in *Meconopsis* and *Platystemon*. Laticiferous sacs recorded in *Cathcartia*, in the root, rhizome, and leaf of *Sanguinaria canadensis* and in *Stylophorum*. Colour and consistency of the latex somewhat variable; white in *Meconopsis*, *Papaver*, *Roemeria*; lemon yellow in *Argemone*; orange in *Chelidonium*; at first watery and somewhat reddish, but later becoming more turbid in *Bocconia*, *Eschscholtzia*, *Glaucium*, *Hypecoum*; watery at first but becoming yellow in *Macleaya* and blood-red in *Sanguinaria*. Latex tending to disappear from the older parts of the plant in *Chelidonium* and *Glaucium*. Experiments with latex tubes of Papaveraceae undertaken by Simon (2103) suggest that these channels do not serve for conduction, although it has been stated by Fedde (676) that the mineral substances in the latex increase its absorptive capacity.

AXIS

STEM (Fig. 20 A, G-H)

A collenchymatous **exodermis** is differentiated in *Argemone mexicana* Linn., *Glaucium flavum* Crantz. and *Macleaya cordata* (Willd.) R. Br. Peripheral part of **cortex** including sclerosed cells in *Argemone mexicana* and *Bocconia* sp. according to Harvey-Gibson and Bradley (915). **Endodermis** not usually

distinct. **Pericycle** generally sclerenchymatous, or at least including a ring of thin-walled, lignified, pitted elements, often with arcs of fibres external to the individual bundles; described by Harvey-Gibson and Bradley as not sclerosed in *Argemone mexicana* and *Romneya trichocalyx* Eastw., and

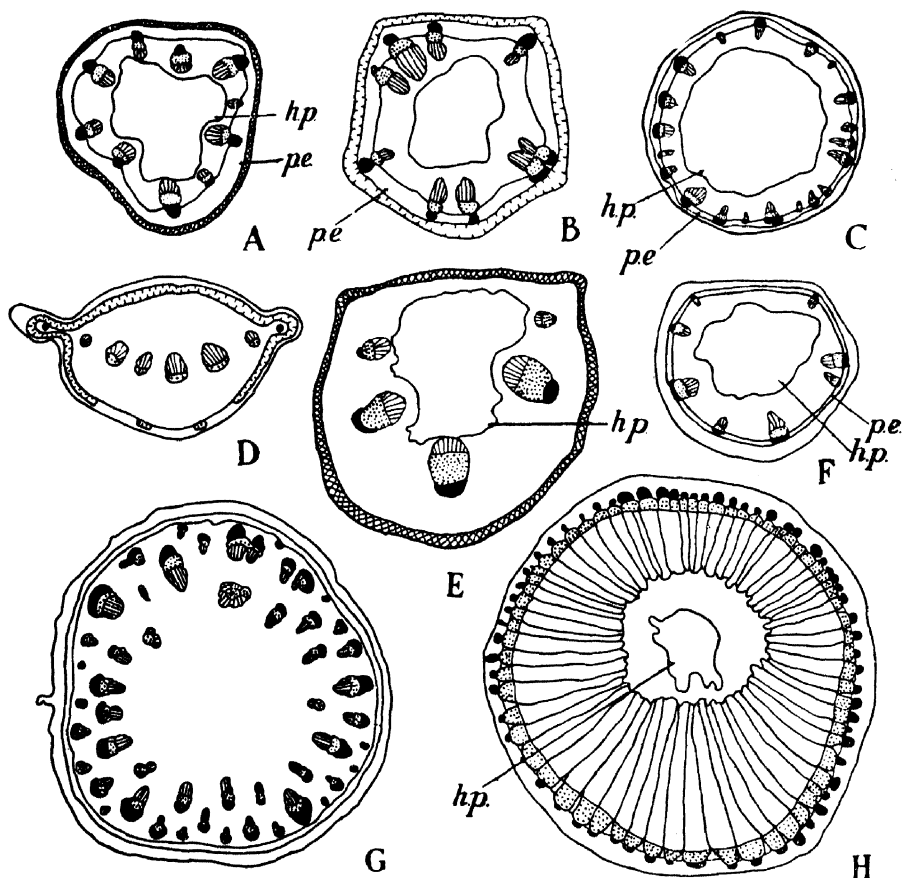


FIG. 20. PAPAVERACEAE, A, D-E, G-H; FUMARIACEAE, B-C and F

A, *Chelidonium majus* Linn. Stem $\times 15$. B, *Fumaria muralis* Koch. Stem $\times 9$. C, *Dicentra spectabilis* Linn. Stem $\times 8$. D, *Romneya trichocalyx* Eastw. Petiole $\times 9$. E, *Chelidonium majus* Linn. Petiole $\times 40$. F, *Dicentra spectabilis* Linn. Petiole $\times 15$. G, *Papaver orientale* Linn. Stem $\times 9$. (The circle in the pericyclic region represents thin-walled, lignified, pitted elements.) H, *Romneya trichocalyx* Eastw. Stem $\times 3$.

h.p. Hollow pith. p.e. Thin-walled, lignified elements with pits.

weakly sclerosed in *Eschscholtzia californica* Cham., *Papaver somniferum* Linn., *P. orientale* Linn. Most Papaveraceae provided with a single ring of collateral **vascular bundles** (Fig. 20 A), the interfascicular tissues between them sometimes tending to become lignified. Numerous bundles arranged in concentric zones, in a manner recalling that of some of the Ranunculaceae, frequently occur in *Papaver* spp., e.g. according to Harvey-Gibson and Bradley (915) in *P. orientale* Linn. (Fig. 20 G) and *P. somniferum* Linn. In the

more woody species, e.g. *Romneya trichocalyx* Eastw. (Fig. 20 H) the vascular bundles are separated by broad primary medullary rays, but are less widely spaced than in the herbaceous species. Vessels with simple perforations.

PEDUNCLE

Usually with a circle of 4–5 vascular bundles in *Papaver dubium* Linn. and *P. somniferum* Linn., but several circles of bundles recorded by Friedel (713) in *P. orientale* Linn. Anatomical structure of the peduncle very constant in *Meconopsis*; cortex narrow, component cells generally with cellulose walls, but sclerenchymatous in *M. chelidonifolia* Bur. et Franch.; pericycle generally including sclerenchyma; pith composed of cells with cellulose walls, becoming hollow; vascular bundles widely separated, arranged in a single circle, their number varying according to the species, as well as in different individuals of the same species, or at different levels in a single peduncle; xylem groups not generally U-shaped (compare 'Stem') except in *M. chelidonifolia* where they are more definitely U-shaped than in the Ranunculaceae.

WOOD (Fig. 25 F–G and I)

Vessels very small (25–50 μ mean tangential diameter) in *Dendromecon rigida* Benth. and *Romneya coulteri* Harv., and with many tracheid-like vessels in the latter, medium-sized in *Bocconia frutescens* Linn.; in short radial multiples and irregular clusters, which form vague to distinct oblique lines in *Dendromecon* and *Romneya*; few, solitary and in radial pairs, and without pattern in *Bocconia*; semi-ring-porous in *Dendromecon*; with spiral thickening in *Dendromecon* and *Romneya*. Perforations simple. Intervascular pitting alternate, rather large in *Bocconia*; pits to ray or wood parenchyma similar to the intervascular pitting in *Dendromecon* and *Romneya*, larger, with wide apertures and often elongated in *Bocconia*. Mean member length about 0.4 mm. **Parenchyma** paratracheal, vasicentric (Fig. 25 F) to sparse; strands of 1–2 cells in *Bocconia* and *Dendromecon*, fusiform cells sometimes predominating. **Rays** all multiseriate, up to 5 and 7 cells wide in *Dendromecon* and *Romneya*, and up to 12 cells in *Bocconia*; commonly more than 2 mm. high; cells all square or upright in *Dendromecon* and *Romneya*, markedly heterogeneous in *Bocconia*, tangential sections showing separate groups of small procumbent cells in each ray surrounded by square to upright cells (Fig. 25 G); with sheath cells; about 3 rays per mm. Dadswell and Record (533) refer to a few large, open, radial canals in *Bocconia*. **Fibres** with numerous, small, simple pits on both radial and tangential walls. Walls moderately thin to rather thick. Mean length 0.6–0.75 mm.

RHIZOME

Described by Holm (1027) as showing a circular band of vascular bundles and interfascicular cambium in *Sanguinaria canadensis* Linn. Sclerenchyma recorded in the pericycle of this species.

ROOT

Primary structure generally diarch. Growth in thickness very limited and confined to the stele in *Sanguinaria canadensis* Linn. according to Holm (1027).

TAXONOMIC NOTES

One of the most interesting anatomical features is the tendency for the vascular bundles in a few species to be scattered. The xylem groups are also occasionally U-shaped. Both these characters suggest affinities with the Ranunculaceae, and therefore with some of the Monocotyledons. The view expressed by Friedel (713, 714) that the presence of a small number of vascular bundles in the peduncle indicates a primitive position within the family seems to have very little to support it, and Friedel himself appears subsequently to have become very uncertain about this suggestion, judging from the remarks in the second of his two papers just cited.

The laticiferous elements are generally believed to be homologous with the secretory cells of the closely related Fumariaceae.

The wood anatomy of *Dendromecon* and *Romneya* is closely similar, but that of *Bocconia* differs strikingly in several vessel characters.

ECONOMIC USES

Opium is the dried latex from the seed capsules of *Papaver somniferum* Linn. The petals of *Papaver rhoeas* Linn. and the dried rhizome of *Sanguinaria canadensis* Linn. are used medicinally.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Argemone, Bocconia, Cathcartia, Chelidonium,* Dendromecon, Eschscholtzia, Glaucium, Macleaya,* Meconella, Meconopsis, Papaver,* Platystemon, Platystigma, Pteridophyllum, Roemeria, Romneya,* Sanguinaria, Stylophorum.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Bocconia, Dendromecon, Romneya.

LITERATURE

(i) *On General Anatomy*

Fedde 675, 676, Friedel 713, 714, 715, 716, 717, Fritsché 725, Harvey-Gibson and Bradley 915, Holm 1027, Simon 2103, Werdemann 2413.

(ii) *On Wood Structure*

Dadswell and Record 533, Record 1843, 1851, Record and Hess 1886.

25. FUMARIACEAE

(FIG. 20 on p. 76)

SUMMARY

A family of herbs, mainly from North Temperate regions, closely related to, and by some authorities included in, the Papaveraceae. Some of its members are scandent. Features of morphological interest include the basal tubers which occur in various species of *Corydalis* such as *C. cava* (L.) Schweigg. et Körte and *C. solida* (L.) Swartz. The morphological nature of the tubers of *C. solida* is somewhat uncertain as they cannot be strictly regarded

as stems or roots. According to Fritsché (725) young tubers arise internally from pre-existing ones. True bulbs occur in *Dicentra cucullaria* (L.) Bernh. It is also noteworthy that the seedlings of certain species of *Corydalis* and *Dicentra* possess only one cotyledon. The primary structure of the root is diarch.

In a general way the anatomical characters of the Fumariaceae are so similar to those of the herbaceous members of the Papaveraceae that there is no need to recapitulate them in detail. The type of **petiole** structure is shown in Fig. 20 F for *Dicentra*, whilst transverse sections of young stems of *Fumaria* and *Dicentra* are illustrated in Fig. 20 B-C. Beyond this it will suffice to say that the most characteristic feature of the family is the presence of **secretory cells** or idioblasts up to 10 mm. long, which have been recorded in different parts of certain species of *Adlumia*, *Corydalis*, *Dicentra*, and *Fumaria*. The nature of the contents of these cells is uncertain. In view of the close affinities of the Fumariaceae and Papaveraceae it seems reasonable to suppose that they are of the same nature as the laticiferous cells of the Papaveraceae.

GENERA DESCRIBED

Adlumia, *Corydalis*,* *Dicentra*,* *Fumaria*.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Fritsché 725, Kloimweder 1246.

26. CRUCIFERAE

(FIG. 21 on p. 80; FIG. 22 on p. 84; FIG. 25 on p. 92)

SUMMARY

(i) GENERAL

A cosmopolitan family consisting predominantly of herbs, but a few species tend to be shrubby. Well-defined, characteristic anatomical features exist throughout the family. **Secretory cells** containing myrosin, which is coagulated and stained red by Millon's reagent, or coloured violet with orcin solution and concentrated hydrochloric acid, are especially noteworthy. They are widely distributed throughout the Cruciferae, but their frequency is partially controlled by nutrition and environment. They may occur in any part of the plant and in practically any of the tissues. The nature and distribution of idioblasts containing myrosin may be of taxonomic value (see 'Leaf'). The **stomata** are surrounded by 3 subsidiary cells of which 1 is usually much smaller than the other 2, the so-called cruciferous type. **Cork** arises in the pericycle or inner part of the cortex of the stem. The interfascicular tissue between the xylem strands of adjacent **vascular bundles** in the stem becomes lignified at a very early stage, so that normal, parenchymatous, primary medullary rays are generally absent. Variations of this basic type of stem structure are described under 'Axis'. **Hairs** are always unicellular, but may be simple, unbranched, Y-shaped, 2-armed, peltate, or

dendroid; and the walls are sometimes encrusted with calcium carbonate. Glandular hairs rare. **Water-storage cells** are common in the epidermis,

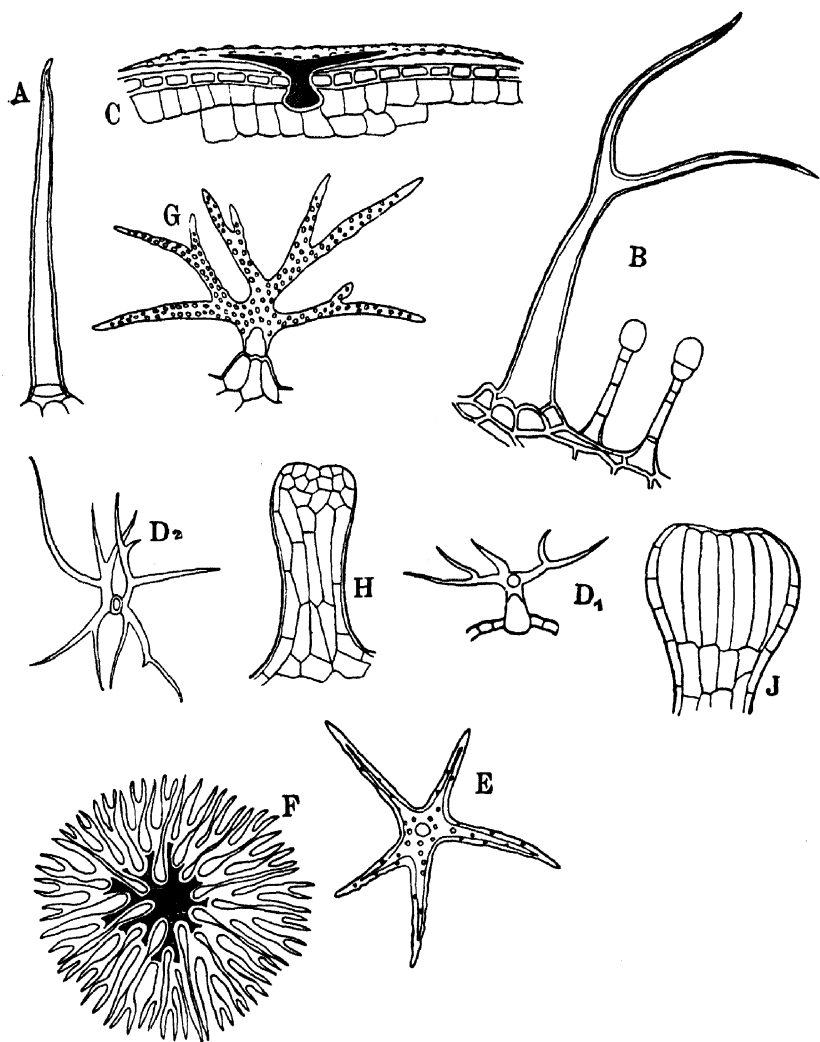


FIG. 21. CRUCIFERAE

A, Simple hair from the upper side of the leaf of *Capsella bursa-pastoris* (L.) Medic. B, Forked hair and glandular hair of *Hesperis glutinosa* Vis. from the floral region. C, Two-armed calcified hair from the leaf of *Cheiranthus cheiri* L. D₁ and D₂, Stellate hairs from the leaf of *Matthiola livida* DC. in surface view and from the side. E, Stellate hair from the lower side of the leaf of *Capsella bursa-pastoris* (L.) Medic. F, Peltate hair of *Alyssum lepidotum* Boiss. G, Dendroid hair from the lower side of the leaf of *Alyssum saxatile* Linn. H and J, External glands of *Matthiola livida*: H, Entire glandular hair seen from the side; J, Longitudinal section through the glandular head.—A, E, and G after Vesque; F after O. Bachmann; the remainder by Solereder.

especially of the leaf. **Crystals** of calcium oxalate very infrequent, but crystals, believed to be related to hesperidin, recorded in *Capsella bursa-pastoris* (L.) Medik. **Anomalous structure** occurs in a few species.

(ii) WOOD

Vessels small, perforations simple, intervacular pitting alternate with horizontal apertures, members very to extremely short. **Parenchyma** paratracheal, extremely sparse. **Rays** up to 2-4 cells wide, sometimes high, heterogeneous. **Fibres** with small bordered pits, extremely short.

LEAF

Mesophyll structure variable; centric in *Anastatica hierochuntica* Linn., *Crambe maritima* Linn., *Moricandia arvensis* (L.) DC. Dorsiventral in leaves on the lower part of the stem of *Capsella bursa-pastoris* (L.) Medik. and *Lepidium sativum* Linn. Upper cauline leaves of the same species with palisade tissue towards both surfaces. Palisade tissue towards both surfaces in *Cakile edentula* (Big.) Hook. Palisade and spongy mesophyll not differentiated in *Cakile maritima* Scop. Wax commonly excreted on both surfaces. Palisade tissue generally consisting of 1-3 layers.

Hairs (Fig. 21 A-J) very variable in form, but always unicellular apart from the relatively infrequent glandular types; frequently calcified. Non-glandular hairs often simple, but branched, T-shaped, and stellate kinds also occur, the T-shaped variety having been recorded in species of *Draba*, *Erysimum*, *Farsetia*, *Lobularia*, and 4-armed ones in *Lesquerella* spp. Glandular hairs, consisting of a multicellular stalk and a head of 1 or more cells, recorded in species of *Anchonium*, *Bunias*, *Chorispora*, *Descurainia*, *Hesperis*, *Matthiola*, *Parrya*, *Sterigma*. Simple and branched hairs occur either separately or together. Glandular hairs generally to be found amongst other kinds. Treitel (2276) found the structure and dimensions of the hairs to be the most important anatomical features for the identification of leaves of different genera and species.

Stomata (Fig. 22 E) typically cruciferous except sometimes, e.g. in *Sabularia*; generally occurring on both surfaces, but, according to Treitel (2276), confined to the lower surface in *Lunaria annua* Linn. (syn. *L. biennis* Moench.) and *L. rediviva* Linn. Stober (2201) found stomata to be more numerous on the cauline than on the rosette leaves of *Capsella bursa-pastoris* and *Lepidium sativum*, but those of rosette leaves larger and more elongated than the ones on the cauline leaves in these 2 species. According to the same author the size and shape of stomata vary considerably not only in these 2 species, but also in different individuals of either of them, or even in different parts of a single leaf. **Epidermis**. Solitary water-storage cells interspersed amongst normal epidermal ones in *Heliophila* spp., *Isatis tinctoria* Linn., *Senebiera coronopus* Poir. Small groups of these cells sometimes present as well in the above species. Water-storage cells form a network on the surface of the leaf in some species, e.g. *Diplotaxis acris* (Forsk.) Boiss., *D. tenuifolia* (L.) DC., *Eremobium aegyptiacum* (Spreng.) Hochreut. (syn. *Malcomia aegyptiaca* Spreng.); *Moricandia arvensis* (L.) DC., *Raphanus sativus* Linn., *Savignya parviflora* (Del.) Webb. The cells in some species form elongated sacs, e.g. *Heliophila* spp. Uniseriate, unbranched groups of cells, smaller than those of the surrounding tissues, recorded by Schweidler (2060, 2061) in the mesophyll of certain species, including *Iberis pinnata* Linn., *I. umbellata* Linn., and *Moricandia arvensis* (L.) DC. Biseriate and branched groups less

frequent. When in the palisade region each series has its long axis at right angles to the epidermis, but parallel to the epidermis when in the spongy mesophyll. No special contents noted in these cells.

Vascular bundles of the larger **veins** nearly always surrounded by collenchyma. Transverse sections through the distal ends of the **petioles** from a random selection of different members of the family revealed 3 main but intergrading types of vascular structure. (i) A single principal bundle accompanied by subsidiary strands in the wings in *Alyssum saxatile* Linn., *Aubrietia deltoidea* (L.) DC. (Fig. 22 B) (main bundle supported by sclerenchymatous masses with wide lumina to the cells), *Cheiranthus cheiri* Linn. (Fig. 22 C), *Draba* sp. (ii) A crescent or U-shaped group of separate bundles in *Armoracia lapathifolia* Gilib. (syn. *Cochlearia armoracia* Linn.) (In this species the xylem vessels in each of the larger bundles form a U-shaped group; bundles strongly supported by sclerenchyma; many scattered subsidiary bundles also present), *Bunias orientalis* Linn. (Fig. 22 K), *Lepidium sativum* Linn. (Fig. 22 A), *Lunaria rediviva* Linn., *Matthiola incana* (L.) R. Br. (a very open arc). (iii) Larger individual bundles of the main U-shaped group, each consisting of a ring or cluster of vascular strands, scattered accessory strands often being present as well, in *Brassica juncea* (L.) Czernjaew, *B. oleracea* Linn. (Fig. 22 F), *Crambe maritima* Linn. (Fig. 22 D), *C. orientalis* Linn. Bundles frequently more numerous at the base than at the distal end of the petioles, e.g. 50–100 present at the base of *Brassica oleracea*. Considerable variation in petiolar vascular structure sometimes occurs in different species of a large genus such as *Brassica*. **Crystals** of calcium oxalate rare, but large ones recorded in a species of *Crambe*, and in *Sisymbrium altissimum* Linn., although seldom present in other members of the Sisymbrieae. **Secretory cells**. Various attempts have been made to classify the Cruciferae according to the frequency and distribution of the myrosin cells or idioblasts. Thus Heinricher (1940) recognized 5 types. (i) Myrosin cells distributed throughout the leaf parenchyma. (ii) Most of the myrosin cells situated in the parenchymatous sheaths around the vascular bundles of the veins; only a small proportion distributed in the mesophyll. (iii) Myrosin cells restricted to certain cells of the sheaths around the vascular bundles of the veins. (iv) Myrosin cells confined to the veins, but occurring only in the mechanical tissue situated on the inside of the parenchymatous sheaths. (v) Myrosin cells occurring in the mesophyll, but predominantly in the sub-epidermis. Heinricher also divided the family into 7 sections according to the distribution of the myrosin cells in the stem.

Schweidler (2060, 2062) adopted a somewhat different arrangement which takes into account the nature of the contents of the idioblasts as well as their distribution. He recognized 3 groups. (i) Exo-idioblastae with chlorophyll-containing idioblasts exclusively in the mesophyll. (ii) Endo-idioblastae with idioblasts containing albumen but no chlorophyll, present exclusively in association with the bundles. (iii) Heteroidioblastae, with idioblasts both in the mesophyll and conducting strands. Using the nature and distribution of the idioblasts as a taxonomic character, Schweidler made suggestions concerning the possible close affinity of certain genera, and indicated that in other instances species now included in a single genus should be separated. Details can best be obtained from his papers, but since the frequency of these bodies can be modified to some extent by varying the nutrition and environmental

conditions, it seems to be desirable that their taxonomic significance should be investigated experimentally before their value is assessed.

AXIS

STEM (Fig. 22 G-J, L)

Epidermis, usually composed of cells with strongly thickened inner walls; sclerotic in *Arabis procurrens* Waldst. et Kit.; 2-layered in *Diplotaxis harra* (Forsk.) Boiss, *Zilla spinosa* (L.) Prantl (syn. *Zilla myagroides* Forsk.). Outer part of primary **cortex** frequently collenchymatous. Palisade chlorenchyma recorded in the outer part of the cortex of desert plants such as *Eremobium aegyptiacum* (Spreng.) Hochreut. (syn. *Malcomia aegyptiaca* Spreng.) and *Zilla spinosa* (L.) Prantl. Vertically elongated, unligified but spirally to reticulately thickened cells present in the outer cortex of the xerophytic species *Oudneya africana* R. Br. Stem furrowed in *Notothlaspi australe* Hook. f., according to Betts (187), the cells below the furrows being smaller than those elsewhere in the cortex and containing abundant chlorophyll. **Cork** of woody species originating in the inner part of the cortex or in the phloem (*Arabis procurrens* and *Aubrietia deltoidea* (L.) DC.). Phellogen in the perennating stems of '*Alyssum arduini*' arising, according to Hollendonner (988), amongst mechanical cells at the bases of the petioles when the leaves become detached; and also between the annual flowering and perennial stems. A second phellogen subsequently arises in the bark around groups of sclereids which then form islands. **Endodermis** well defined in species of *Brassica*, *Cap-sella*, *Kerneria*, *Lepidium*, *Nasturtium*, *Sinapis*, and other genera. **Pericycle** including well-developed strands or, in many genera including *Brassica*, *Draba*, *Lesquerella*, and *Lunaria*, a continuous ring of fibres.

Vascular structure showing a considerable range of variation (see below). Vessels of variable diameter; perforations simple. Wood fibres with simple pits. **Pith** generally parenchymatous, frequently occupying a large proportion of the total diameter of the stem, becoming hollow in many species; septate in old branches of *Diplotaxis harra* (Forsk.) Boiss., outer portion prosenchymatous in *Zilla spinosa* (L.) Prantl. **Adventitious shoots**, stated by Wilson (2438) to be exogenous in origin, arise from roots of *Nasturtium austriacum* Cranz. (syn. *Rorippa austriaca* Spach.).

The **xylem** and associated tissues of the Cruciferae exhibit a considerable range of variation, which is largely associated with differences in the maximum transverse area attained by the stems of different species (Fig. 22 G-J, L). Attention was drawn to this range of structure by Dennert, who recognized 7 distinct types which were cited by Schulz (2055). The following summary was, however, drawn up after examining the slides in the collection at Kew. In species with thin stems the xylem constitutes a closed cylinder as seen in transverse section, the vessels being evenly distributed. This type of structure is accompanied by a considerable reduction or absence of recognizable medullary rays. It occurs, for instance, in *Alyssum spinosum* Linn., *Arabis albida* Stev., *Draba* sp., *Iberis sempervirens* Linn. (Fig. 22 G), *Isatis tinctoria* Linn., *Lepidium sativum* Linn. (old stems), *Matthiola incana* (L.) R. Br. In the above instances the cambium has the form of a continuous ring. This applies also to species of *Brassica*, *Crambe*, *Lunaria*, and probably to many other genera as well, but in these plants the xylem does not form a continuous

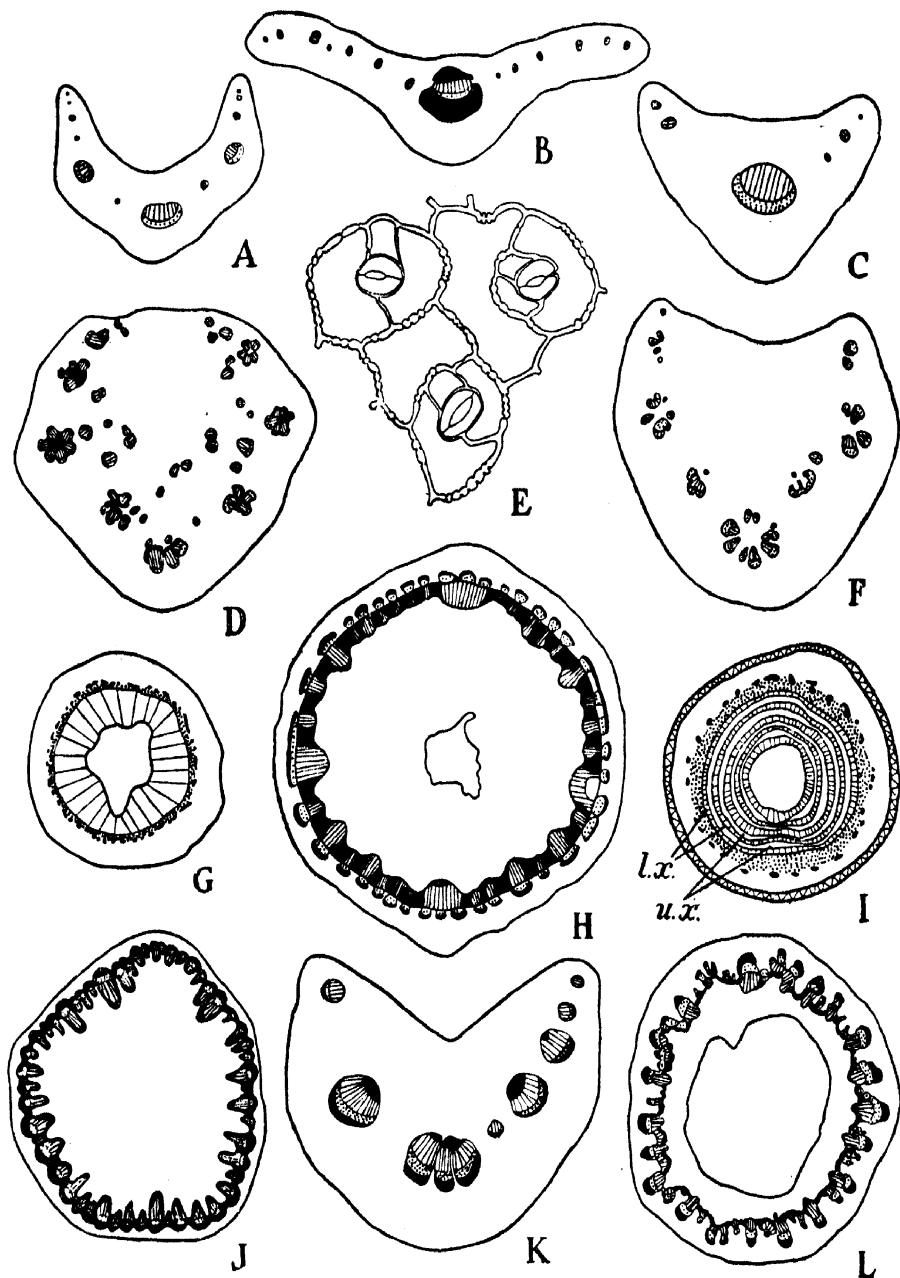


FIG. 22. CRUCIFERAE

A, *Lepidium sativum* Linn. Petiole $\times 15$. B, *Aubrieta deltoidea* (L.) DC. Petiole $\times 19$. C, *Cheiranthus cheiri* Linn. Petiole $\times 15$. D, *Crambe maritima* Linn. Petiole $\times 4$. E, *Iberis sempervirens* Linn. Stomata on lower surface $\times 167$. F, *Brassica oleracea* Linn. Petiole $\times 9$. G, *Iberis sempervirens* Linn. Stem $\times 10$. H, *Lunaria rediviva* Linn. Stem $\times 8$. I, *Alyssum spinosum* Linn. Stem $\times 10$. J, *Bunias orientalis* Linn. Stem $\times 3$. K, *B. orientalis* Linn. Petiole $\times 10$. L, *Armoracia lapathifolia* Gilib. Stem $\times 9$.

l.x. Lignified xylem. u.x. Unlignified xylem.

ring since the primary bundles remain separated from one another by lignified sclerenchymatous tissues, containing no vessels but nevertheless produced by the cambium. This sclerenchymatous tissue could be interpreted either as secondary xylem devoid of vessels or as lignified medullary ray tissue produced by the cambium. In young stems of *Brassica* and certain other genera the cambium is at first confined to the primary bundles, but subsequently extends into the interfascicular zones and so gives rise to the structure just described. In other instances the primary bundles remain individually distinct, but are separated from one another by interfascicular sclerenchyma produced by lignification of the primary tissues, the cambium taking no part in its formation. This structure is to be seen in young stems of *Alyssum saxatile* Linn. and *Brassica juncea* (L.) Czernjaew as well as in older material of *Bunias orientalis* Linn. (Fig. 22 J). Amongst the species which have been examined its maximum development is attained in *Armoracia lapathifolia* Gilib. (syn. *Cochlearia armoracia*) (Fig. 22 L), where the cambium strands are still confined to the separate bundles even in fully matured specimens.

Another interesting feature of the xylem is provided by species in which the vessels of the first-formed wood are very minute compared with those in the wood of older material. This is to be seen especially in species with thin or wiry stems such as *Arabis albida* Stev., *Aubrietia deltoidea* (L.) DC., and *Iberis sempervirens* Linn. Species with more fleshy stems, such as *Bunias orientalis* Linn., sometimes exhibit this feature as well, but to a less marked extent. In plants such as *Alyssum spinosum* Linn. (Fig. 22 I), there are alternating concentric zones of xylem with large and small vessels respectively, the smaller ones being embedded in zones of relatively thin-walled ground tissue. In these instances it looks as if the cambium periodically produces a 'juvenile' form of xylem. In *Alyssum spinosum* the smaller vessels are spirally thickened, whilst the larger ones are provided with large, horizontal, bordered pits. The structure of the wood in old stems of *Alyssum saxatile* Linn. is also somewhat similar, since the xylem includes irregular islands of parenchyma. The vessels in the first-formed wood in this species are minute. (See also 'Anomalous Structure'.)

It must be emphasized that, although the variation in the vascular structure of the stems of the Cruciferae may serve as an aid to the identification of genera and species, similarity of structure must not necessarily be regarded as evidence of affinity. The structure appears to be related to the mechanical and physiological requirements of the different species rather than to their taxonomic relationships.

WOOD (Fig. 25 H and L)

Vessels small, mostly solitary, but with some radial multiples and clusters (Fig. 25 L), sometimes with a slight tangential pattern in *Brassica*; seldom touching the rays; about 40–50 per sq. mm. Perforations simple. Inter-vascular pitting alternate, sometimes elongated horizontally, with horizontal apertures; sometimes with striations due to coalescent apertures; pits to parenchyma similar. Mean member length 1.8–2.4 mm. **Parenchyma** paratracheal, limited to rare cells about the vessels (Fig. 25 L). **Rays** up to 2–4 cells wide; less than 1 mm. high in *Schouwia* (1493), more than 2 mm. in

Brassica; uniseriates few; 2-6 rays per mm.; markedly heterogenous and composed mainly of square to upright cells. **Fibres** with small bordered pits, equally numerous on both radial and tangential walls. Mean length about 0.4 mm. (1493).

Root

Primary structure usually diarch, but tetrarch structure recorded in *Cochlearia*. The layer of cells immediately external to the **endodermis** has characteristic thickenings in a considerable number of unrelated genera, but none have been recorded in others. Adventitious roots, stated to be exogenous in origin, arise from subterranean stems or stems in contact with the soil in *Nasturtium austriacum* Cranz (syn. *Rorippa austriaca* Spach.) according to Wilson (2438).

ANOMALOUS STRUCTURE

Concentric zones of unlignified xylem present in the stems of *Alyssum spinosum* Linn., *Brassica fruticulosa* Cyrillo, and *Vella spinosa* Boiss. Ground-work of wood composed of irregular masses of lignified and unlignified tissue in *Alyssum saxatile* Linn. Scattered phloem islands recorded by Pfeiffer (1712) in the xylem of certain species of *Cochlearia* Linn., *Brassica* Linn., and *Raphanus* Linn. Medullary bundles, sometimes concentric in structure, occur in the rhizome of *Armoracia lapathifolia* Gilib. (syn. *Cochlearia armoracia* Linn.) and *Raphanus sativus* Linn. Secondary interxylary bundles said to occur in the unlignified xylem of the rhizome of *Armoracia lapathifolia* and in the root of *Brassica napus* Linn., *B. campestris* Linn. var. *rapa* Harm. (syn. *B. rapa* Linn.), and *Raphanus sativus* Linn. Cortical bundles recorded in *Eruca sativa* Mill. and *Lepidium latifolium* Linn. An inner cambium recorded in the pith of '*Alyssum arduini*'.

ECONOMIC USES

Useful vegetables such as cabbages, cauliflowers, turnips, swedes, &c., are obtained from the genus *Brassica*. The seeds of other species of *Brassica* yield commercial oils and other products such as Rape, Colza, and Mustard. The family also includes the horseradish (*Armoracia lapathifolia* Gilib.) and Woad (*Isatis tinctoria* Linn.).

The fleshy root of the horseradish (*Armoracia lapathifolia*) is bounded externally by a few layers of thin-walled cork cells. A broad layer of spongy tissue is present on the inside of the phellogen and extends inwards to a rather indistinct layer of cambium. The spongy tissue is composed of axially elongated thin-walled parenchymatous cells, appearing circular in transverse sections except where compressed against adjacent cells. Occasional, usually isolated, stone cells occur in the spongy tissue immediately within the phellogen. The spongy tissue probably represents the cortex and phloem, but there is no distinct line of demarcation between the two. Xylem consisting of a broad region of isolated or small groups of vessels up to 60 or 70 μ in diameter, embedded in spongy parenchymatous ground tissue. Vessels provided with horizontal bordered pits and simple perforations. Groups of meristematic cells occur in association with and sometimes partly or wholly surround individual vessels or vessel clusters. Strands of similar, actively dividing cells

also occur in the spongy ground tissue independently of the vessels. These meristematic cells probably represent centres of proliferation of the parenchymatous tissue rather than true cambial regions. Medullary rays absent. Centre of the root occupied by a layer of very lacunar, parenchymatous pith.

The enlarged, tuberous portion of the stem of *Brassica oleracea* Linn. var. *gongylodes* Linn., known as Kohlrabi, is somewhat anomalous in structure. The normal circle of bundles is very poorly developed, whilst the primary rays are exceptionally broad and consist of thin-walled parenchyma. The greater part of the tissue is made up of pith with a system of concentric bundles embedded in it. The medullary bundles coalesce with one another and are continuous with the normal bundle system of the stem at the base and apex of the swollen portion. The developmental anatomy of Kohlrabi has been described by Orsos (1640).

TAXONOMIC NOTES

A well-defined family of herbs and small shrubs with several distinctive anatomical characters. One of the most interesting is the universal occurrence of myrosin cells, which are sometimes stated to be homologous with the laticiferous elements of the Papaveraceae and other related families.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Alyssum,* Anastatica, Arabis, Aubrietia,* Brassica,* Bunias,* Cakile, Cardamine, Cheiranthus,* Cochlearia,* Crambe,* Diplotaxis, Draba,* Eremobium, Eruca, Goldbachia, Heliophila, Iberis,* Isatis,* Kerneria, Lepidium,* Lesquerella, Lunaria,* Matthiola,* Moricandia, Nasturtium, Notothlaspi, Oudneya, Peltaria, Raphanus, Savignya, Senebiera, Sinapis, Sisymbrium, Subularia, Vella, Zilla.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Brassica,¹ (Schouwia).²

LITERATURE

(i) On General Anatomy

Betts 187-90, Boodle 232, Bunton 309, Heinricher 940, Hollendonner 988, Orsos 1640, Pfeiffer, H. 1712, Sabnis 1977, Schulz 2051-3, 2055, Schweidler 2060-2, Simmonds 2101, Soeding 2157, Starr 2188, Stober 2201, Treitel 2276, Wilson 2438, Wright 2475, Zohary and Fahn 2511.

(ii) On Wood Structure

Messeri 1493.

27. CAPPARIDACEAE

(FIG. 23 on p. 88; FIG. 24 on p. 90; FIG. 25 on p. 92; FIG. 26 on p. 96)

SUMMARY

(i) GENERAL

This mainly tropical family consists of herbs, shrubs, and small trees, while a few lianes are included in *Cadaba*, *Capparis*, and other genera. Very few

¹ *Brassica oleracea* var. *ramosa* (DC.) Alefeld.

² *Schouwia schimperi* Jaubert et Spach. From the description given by Messeri (1493).

characters are constant throughout the family. The **stomata** are ranunculaceous. **Crystals** of calcium oxalate are usually small and clustered or prismatic; large solitary crystals rare, but recorded in *Forchhammeria* spp.

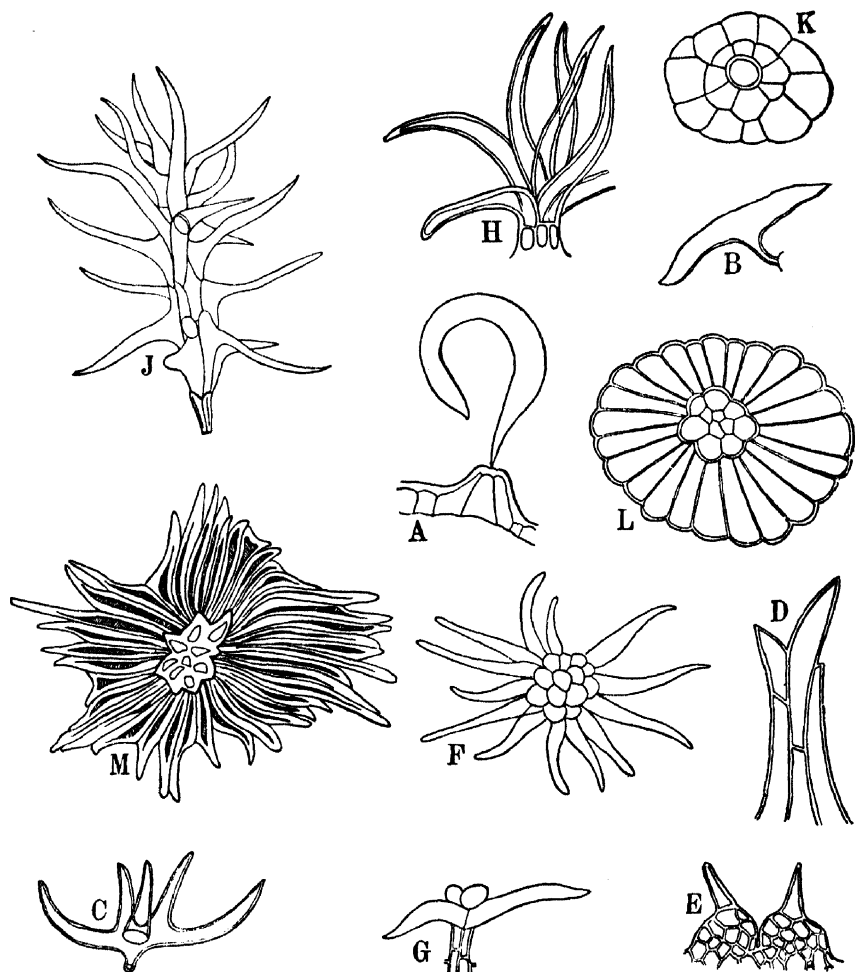


FIG. 23. CAPPARIDACEAE

Hairs of: A, *Capparis spinosa* L.; B, *C. quiniflora* DC.; C, *C. zeylanica* L.; D, *Cadaba capparoides* DC.; E, *Capparis verrucosa* Jacq.; F-G, *Steriphoma paradoxum* (Jacq.) Endl.; H, *Capparis ferruginea* L.; J, *C. domingensis* Spreng.; K, *Cadaba farinosa* Forsk.; L, *Atamisquea emarginata* Miers; M, *Capparis breymia*, Jacq.—J, By Solereder; the rest after Vesque.

Myrosin cells have been observed in *Capparis*, *Cleome*, *Gynandropsis*, and *Polanisia*. **Anomalous structure** occurs in certain genera.

(ii) WOOD

Vessels very small to medium-sized, often in clusters or long radial multiples, perforations simple, intervascular pitting alternate, small and vestured, pits to parenchyma similar, members moderately to extremely short;

small tracheid-like members sometimes numerous. **Parenchyma** paratracheal, usually sparsely vasicentric; fusiform cells often numerous and occasionally forming bands; sometimes storied. **Rays** up to 2-5 cells wide, apart from interfascicular rays when present, typically homogeneous or nearly so, but sometimes composed entirely of square to upright cells. **Fibres** with small simple pits, moderately to extremely short, sometimes storied. **Included phloem** of the 'concentric' type present in some genera.

LEAF

Dorsiventral, isobilateral, or centric.

Hairs (Fig. 23 A-M).

(a) Simple unicellular. (i) Short, usually with thick walls, in *Boscia octrandra* Hochst., *B. salicifolia* Oliv., *Capparis cynophallophora* Linn., and *Maerua crassifolia* Forsk. (ii) Long in *Capparis mollis* H.B. et K. and *Stixis suaveolens* (Roxb.) Pierre. (iii) Ribbon-shaped in *Capparis rothii* Oliv. (iv) Thin-walled, ascus-shaped hairs, with wide lumina and pointed at both ends in *Capparis galatea* Fres., *C. rupestris* Sibth. et Sm., *C. sarmentosa* Cunningh., *C. spinosa* Linn. (v) Malpighian hairs (Fig. 23 B) in *Capparis quiniflora* DC. and *C. zeyheri* Turcz. (vi) Many-rayed hairs (Fig. 23 c) in *Capparis avicenniaefolia* H.B. et K., *C. dealbata* DC., *C. diversiflora* Wight et Arn., *C. erythrocarpa* Isert., *C. foetida* Bl., *C. heyneana* Wall., *C. horrida* Linn., *C. moonii* Wight., *C. tenera* Dalz., and *C. zeylanica* Linn.

(b) Uniseriate hairs in *Capparis citrifolia* Lam., *C. lanceolaris* DC., and *C. tomentosa* Lam.

(c) Emergences resembling shaggy hairs in *Cadaba capparoides* DC. (Fig. 23 D), *C. indica* Lamk., and *C. scaposa* DC. (syn. *C. papillosa* Steud.).

(d) Short, shaggy hairs in *Morisonia americana* Linn.

(e) Stellate hairs. (i) With ray cells all lying in the same plane in *Steriphoma paradoxum* (Jacq.) Endl. (Fig. 23 F-G) and *S. peruvianum* Spruce. (ii) Brush-shaped with ray cells radiating in all directions in *Capparis angustifolia* H.B. et K., *C. indica* Fawcett et Rendle (syn. *C. breynia* Jacq.), *C. detonsa* Triana et Planch., *C. ferruginea* Linn. (Fig. 23 H), *C. incana* H.B. et K., and *C. yco* Mart. (iii) Candelabra hairs (Fig. 23 J) in *Capparis domingensis* Spreng.

(f) Peltate hairs of various types in certain species of *Atamisquea* (Fig. 23 L), *Cadaba*, *Capparis* (Fig. 23 M), *Morisonia*.

(g) Glandular hairs common in the Cleomeae, but rare in the Cappareae.

Variations in the striation of the cuticle stated to be of taxonomic value. Lower **epidermis** papillose in species of *Cleome*, *Crataeva*, *Isomeris*, and *Wislizenia refracta* Engelm.; locally papillose in *Courbonia glauca* DC. Epidermal cells sclerosed in *Capparis yco* Mart.; outer walls perforated in *Capparis baducca* Linn. **Hypoderm** recorded in *Forchhammeria* and some species of *Capparis*. **Stomata** ranunculaceous in the mature leaf; generally present on both surfaces of isobilateral or centric leaves, but usually confined to the lower surface in dorsiventral leaves. **Mesophyll** centric or dorsiventral. Centric structure recorded in certain species of *Boscia*, *Cadaba*, *Capparis*, *Cleome*, *Courbonia*, *Maerua*. Dorsiventral in certain species of *Boscia*, *Cadaba*, *Capparis*, *Crataeva*, *Maerua*, *Morisonia*, *Ritchiea*, *Roydsia*, *Steriphoma*,

Thylachium, *Tovaria*. Mesophyll consisting wholly of short palisade tissue in *Capparis galatea* Fresen. and *Cadaba glandulosa* Forsk. Fine transparent striae, formed by a peculiar fissuring of the leaves on drying, occur in certain species of *Capparis* and *Forchhammeria*. Various shaped sclerenchymatous cells (Fig. 24 B-C) frequently present in the mesophyll of certain species of *Boscia*, *Cadaba*, *Capparis* (lowest layer of cells in the spongy parenchyma sclerosed in *C. zeylanica* Linn. (Fig. 24 A)), *Courbonia*, *Niebuhrria*, *Thylachium*.

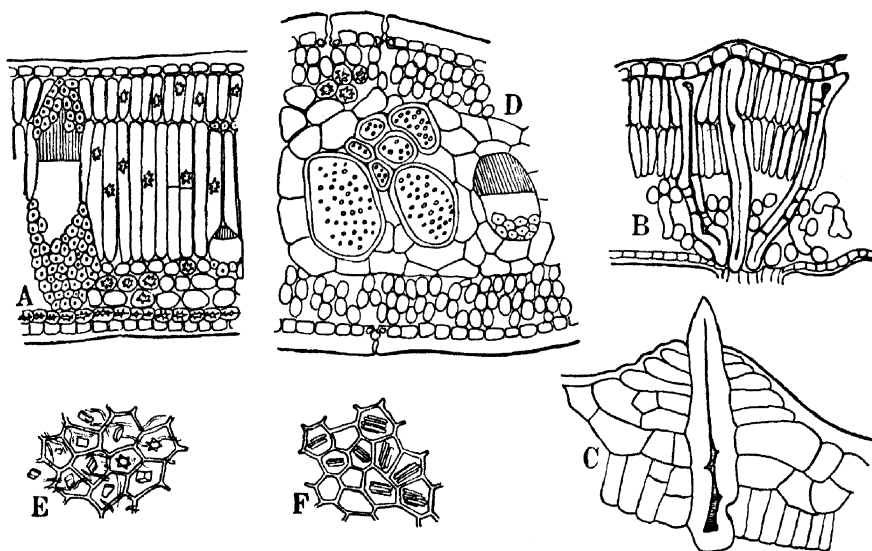


FIG. 24. CAPPARIDACEAE

A, Transverse section through the leaf of *Capparis zeylanica* L. B, Transverse section through the leaf of *Capparis adoratissima* Jacq., with elongated idioblasts converging towards the base of a hair. C, Idioblast of the leaf of *Capparis domingensis* Spreng. D, Transverse section of the leaf of *Capparis galeata* Fres. with reservoir-tracheids. E, Upper epidermis of the leaf of *Capparis cynophallophora* L. with crystals of gypsum. F, Upper epidermis of the leaf of *Capparis polyantha* Tr. et Pl., likewise containing crystals of gypsum.—C, By Solereder; the remainder after Vesque.

Sclerenchymatous cells sometimes extending between the epidermal cells and thus coming into contact with the leaf surface in *Capparis* and *Boscia* spp.

Smaller **veins** nearly always embedded in the mesophyll and sometimes accompanied by sclerenchyma or collenchyma; vertically transcurrent in *Morisonia*; the smaller veins of *Capparis yca* Mart. and *C. zeylanica* Linn. also become vertically transcurrent owing to the development of sclerenchyma on both sides of the vascular bundles. Veins in certain species of *Cadaba* and *Capparis* end in pitted storage tracheids (Fig. 24 D). **Midrib** usually with bundles arranged in a straight band or in an arc with the convex surface towards the lower side; provided with a ring of bundles in *Capparis pachaca* H.B. et K., *Morisonia*, and *Steriphoma*, the ring being formed by the presence of a second arc of bundles having the xylem and phloem inversely orientated.

Petiole, in transverse sections through the distal end of the limited material examined at Kew, exhibiting the following types of vascular structure. A small crescent of very closely placed vascular bundles with strongly incurved ends in '*Capparis linearis* Jacq.' (Fig. 26 B); similar, but more clearly dissected

into separate bundles which form an almost closed cylinder in *Steriphoma ellipticum* (DC.) Spreng (Fig. 26 A); a wide but shallow arc of about 14 individually distinct bundles in *Cleome spinosa* Jacq. (Fig. 26 D); a solitary arc but with the ends detached so as to appear as distinct strands, and with the conspicuous xylem vessels closely packed in very definite radial rows in *Crataeva religiosa* Forst. (Fig. 26 C).

Crystals mostly secreted in the form of solitary prisms or clusters in the mesophyll of certain species of *Capparis*. Solitary crystals occur throughout the epidermis in species of *Cadaba*, *Capparis* (Fig. 24 E-F), *Cleome*, *Forchhammeria*, *Maerua*, *Morisonia*, *Niebuhrria*. The crystals not always composed of the same chemical substance. Sphaero-crystalline masses of gypsum occur as wart-like elevations of the leaf in *Cladostemon kirkii* (Oliv.) Pax et Gilg and *Thylachium panduraeforme* (L.) Juss. and large clustered crystals of gypsum in the mesophyll of certain species of *Capparis*. Small rhomboid, octahedral, or rounded crystalloids present in the epidermis and ground tissue of the petiole of *Boscia*; colourless, refractive, calcareous deposits recorded in *Capparis micrantha* A. Rich and other members of the same genus. **Myrosin cells** (see also 'Axis'), in *Capparis*, *Cleome*, *Gynandropsis*, *Polanisia*, occur either free in the mesophyll or accompany the vascular bundles in the veins; shape not very distinct from that of adjacent cells except for a tendency to be vertically elongated and sometimes arranged in vertical groups in the cortex. Myrosin also reported by Exbrayat-Durivaux (669) to occur in seedlings of *Capparis spinosa* Linn., *Cleome* spp., and *Dactylaena micrantha* Schrad.

AXIS

YOUNG STEM (Fig. 26 E)

Cork originating in the epidermis in *Crataeva*, in the sub-epidermis in *Cadaba glandulosa* Forsk., and at various points in the cortex in *Capparis*. Cork cells often remaining thin-walled, but becoming unilaterally thickened in *Crataeva*. **Aerenchyma** arising in the innermost part of the primary cortex of the lower part of the stem of specimens of *Cleome spinosa* Jacq. from swampy habitats. Primary **cortex** with groups of stone cells in *Crataeva* and *Forchhammeria*, those in the latter genus being especially numerous and filled with large solitary crystals of calcium oxalate. Stone cells in young stems of *Capparis baducca* Linn. arranged in a closed ring. **Pericycle** including strands of fibres alternating with stone cells to form a closed ring in *Cadaba glandulosa* and *Roydsia* or incomplete rings in *Capparis* and *Crataeva*. Isolated groups of stone cells reported by Sabnis (1977) to occur in species of *Capparis* and *Cleome*. Solitary crystals of calcium oxalate present in the pericyclic stone cells of *Cadaba* and *Forchhammeria*. Secondary **phloem** devoid of fibres in nearly all investigated genera, but well-developed fibres recorded in *Boscia rehmanniana* Pest by Adamson (6), especially in old material. **Myrosin cells** (see also 'Leaf') recorded in the primary and secondary cortex of the stem and root in *Capparis*, *Cleome*, *Gynandropsis*, *Polanisia*. **Crystals**, see under 'Leaf', 'Cortex', and 'Pericycle'.

WOOD (Fig. 25 A-E, J-K, and M)

Vessels very small (25–50 μ mean tangential diameter), e.g. in some species of *Atamisquea*, *Isomeris*, and *Maerua*, to medium-sized (100–200 μ), e.g. in

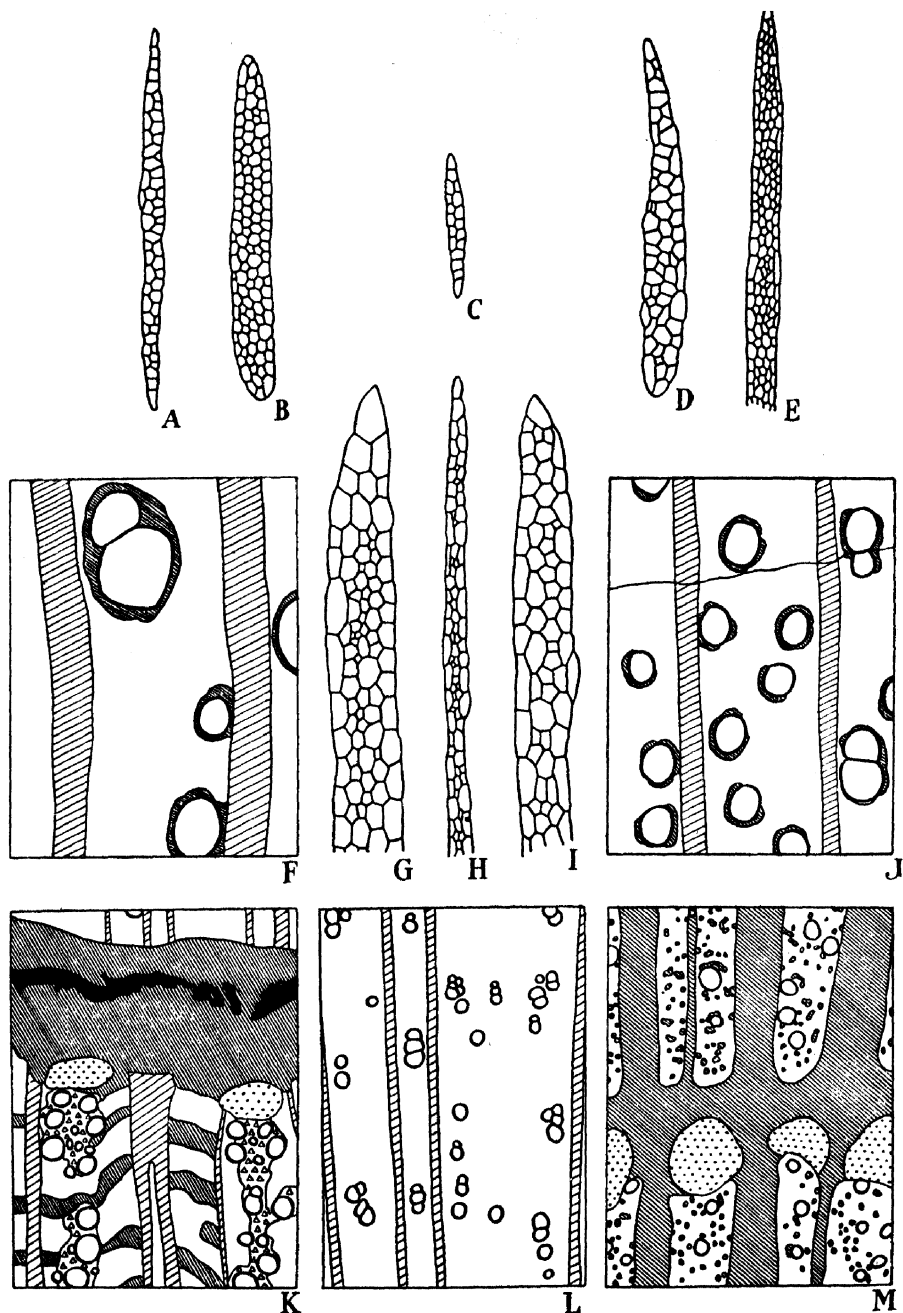


FIG. 25. CAPPARIDACEAE, A-E, J-K, and M; PAPAVERACEAE, F-G and I;
CRUCIFERAE, H and L

A, *Atamisquea emarginata* Miers. B, *Crataeva religiosa* Forst. C, *Boscia senegalensis* Lam. D, *Cadaba trifoliata* Wight et Arn. E, *Isomeris arborea* Nutt. F, *Bocconia frutescens* Linn. G, *B. frutescens* Linn. H, *Brassica oleracea* Linn. var. *ramosa* (DC.) Alefeld. I, *Dendromecon rigida* Benth. J, *Crataeva religiosa* Forst. K, *Cadaba trifoliata* Wight et Arn. L, *Brassica oleracea* Linn. var. *ramosa* (DC.) Alefeld. T.S. M, *Forchhammeria longifolia* Standl. T.S.

some species of *Crataeva* and in *Maerua linearis* (DC.) Pax (syn. *Niebuhria linearis* DC.); solitary and in short radial multiples without any pattern in *Apophyllum*, *Atamisquea*, *Bucholzia*, *Capparis* (most species), *Crataeva*, *Maerua rosmarinoides* (Sond.) Gilg et Benedict and *Maerua linearis* (but not in other species of *M.*); with a marked radial pattern in *Boscia*, *Cadaba* (Fig. 25 κ), *Maerua* (most species), and *Steriphoma*; with both radial multiples and clusters arranged in tangential lines in *Isomeris*; commonly in clusters in *Apophyllum*, *Cadaba*, *Capparis*, *Cleome*, and *Steriphoma*, the clusters sometimes consisting of 1 or 2 moderate-sized vessels surrounded by many minute, tracheid-like vessels, e.g. in *Cadaba trifoliata* W. et A. and *Capparis aphylla* Roth.; 2–35 per sq. mm.; spiral thickening reported (Solereder 2158) in the tips of the members in *Cleome*. Perforations simple, horizontal, or oblique and often vertical on the side-walls of the smallest members; imperfect vessel members very common in the genera with clustered vessels. Intervascular pitting alternate, very small to minute, obscurely vested (Bailey 73, 78); pits to ray cells similar to the intervacular pitting. Often filled with solid deposits. Mean length 0.15–0.3 mm. **Parenchyma** paratracheal, except in *Cadaba* and *Forchhammeria*; most commonly vasicentric and sparse (Fig. 25 j); sometimes more abundant and aliform or confluent, e.g. in *Capparis* p.p. (Janssonius 1154), *Crataeva* p.p., *Maerua* p.p., and *Steriphoma*; apotracheal, in 4-seriate bands composed mainly of fusiform cells in *Cadaba*, and diffuse in *Forchhammeria*; in *Bucholzia coriacea* Engl. the parenchyma is of 2 types, relatively thick-walled strands of 2 cells about the vessels (vasicentric) and broad (4), continuous bands of thin-walled fusiform cells; in numerous concentric bands in *Steriphoma* (Record and Hess 1886), terminal bands present in some species of *Capparis* and *Crataeva*. Strands typically of 1–2 cells; fusiform cells common in *Bucholzia*, *Cadaba*, *Crataeva*, and *Isomeris*. Tending to be storied in *Atamisquea*, *Capparis*, e.g. *C. salicifolia* Gris. (Cozzo 493), *Crataeva*, *Isomeris*, and *Maerua* p.p. **Rays** usually up to 2–5 cells wide and seldom more than 1 mm. high; occasionally up to 6 cells in *Crataeva* and *Isomeris*; very wide and high interfascicular rays present in *Forchhammeria*; uniseriate typically few, except where the maximum width is only 2 or 3 cells, e.g. in species of *Atamisquea*, *Boscia*, *Bucholzia*, *Morisonia*, *Steriphoma*, and *Stuebelia* (Record and Hess 1886), and composed of square cells in *Atamisquea*, but mostly of procumbent cells in *Boscia* and *Bucholzia*; 3–9 rays per mm.; typically homogeneous, though with occasional single rows of square cells in *Boscia* and some species of *Capparis* and *Steriphoma*; composed almost entirely of square cells in *Atamisquea*, *Cadaba*, and *Maerua rosmarinoides*, distinctly heterogeneous in *Cleome* (Chattaway 376). Crystals present in unspecialized cells in *Atamisquea*, *Capparis* (Janssonius 1154), *Morisonia*, and *Steriphoma* and occurring in almost every ray cell in *Atamisquea emarginata* Miers. **Fibres** typically with very small simple or faintly bordered pits, but with small, distinctly bordered pits in *Forchhammeria*; pits mostly on the radial walls except in *Forchhammeria* and *Isomeris* and usually absent from the walls touching vessels. Occasionally septate in *Morisonia* (Chattaway 376). Walls thin to thick; sometimes with alternating bands of thinner and thicker-walled fibres in *Capparis*. Occasionally storied. Mean length 0.2–0.9 mm. **Included (interxylary) phloem** of the 'concentric' type (c.l. *circumvallatum*) occurs in certain genera (see p. 94).

ANOMALOUS STRUCTURE

Anomalous stem structure, consisting of successive rings of growth, recorded in *Boscia* (Adamson 6), *Cadaba*, *Forchhammeria*, *Maerua*, *Stixis*; typically with successive layers of secondary xylem containing numerous rays and often including more than one growth ring, but in *Forchhammeria* with successive bundles of xylem and phloem repeating the structure of the young stem, separated by large interfascicular rays. Secondary bundles arise in the phloem in *Maerua crassifolia* Forsk. (syn. *M. uniflora* Vahl.) and in the pericycle internally to the sclerenchyma in *Forchhammeria trifoliata* Radlk., but externally to the pericyclic fibres in *Forchhammeria pallida* Liebm. Phloem of secondary growth zones forming continuous rings in *Forchhammeria* and *Maerua*.

In *Boscia rehmanniana* Pest. according to Adamson (6), a succession of irregular zones of phloem and xylem is produced from secondary cambia arising externally to and at various distances from the phloem. The secondary cambia nearest to the phloem behave normally by developing in a centrifugal manner. Those farther out are in the form of 2 active zones which respectively develop in centrifugal and centripetal directions, the new tissues formed in the last of these ways exhibiting inverse orientation. Centripetal development ceases sooner than the centrifugal. By repetition of this mode of growth the wood assumes a complex structure. When the cambia cease to be active they often become decomposed with the formation of gum, and subsequently split along these lines of weakness. The branches are also easily detached from the trunk along the planes of cleavage. *Capparis* lianes are normal in structure.

TAXONOMIC NOTES

The presence of myrosin cells in certain genera suggests that the Capparidaceae and Cruciferae may have affinities with one another, and also with the Resedaceae where similar cells also occur. The considerable diversity of structure in the family is partly correlated with the various habits of the plants. Pax and Hoffmann (1678) include *Koeberlinia* in this family, but this does not appear to be supported by its anatomical structure. It is described in this book under Koeberliniaceae (p. 331). The wood anatomy of the only species available of *Forchhammeria* (*F. longifolia*) differs significantly from the rest of the family.

ECONOMIC USES

Capers are the pickled flower-buds of *Capparis spinosa* Linn.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Boscia, *Cadaba*, *Capparis*,* *Cladostemon*, *Cleome*,* *Courbonia*, *Crataeva*,* *Forchhammeria*, *Gynandropsis*, *Isomeris*, *Maerua*, *Morisonia*, *Polanisia*, *Ritchiea*, *Steriphoma*,* *Thylachium*, *Tovaria*, *Wislizenia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Apophyllum, *Atamisquea*, *Boscia*, *Bucholzia*, *Cadaba*, *Capparis*, (*Cleome*),

Crataeva, *Forchhammeria*, *Isomeris*, *Maerua*, (*Morisonia*), (*Niebuhreria*), (*Roydsia*), (*Steriphoma*), (*Stuebelia*).

LITERATURE

(i) *On General Anatomy*

Adamson 6, Exbrayat-Durivaux 669, Pax and Hoffmann 1678, Sabnis 1977.

(ii) *On Wood Structure*

Bailey 73, 78, Benoist 169, Burgerstein 310, Chalk and Chattaway 362, Chattaway 376, Cozzo 493, Desch 574, Howard 1088, Janssonius 1154, Kanehira 1206, 1209, Lecomte 1334, Pfeiffer, H. 1712, Record 1783, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Williams 2430.

28. RESEDACEAE

(FIG. 26 on p. 96)

SUMMARY

An herbaceous family which occurs in the North Temperate zone, particularly in the Mediterranean region. The **hairs** are simple, unicellular trichomes, frequently rounded at the apex. Structures intermediate between hairs and papillae also occur in some species and are believed to serve for the storage of water. **Myrosin cells** are especially characteristic of the family, and sometimes occur in association with the stomata. The **epidermis** of the leaf consists of cells of 2 distinct sizes. The **stomata** are ranunculaceous. The **mesophyll** is not clearly differentiated into spongy and palisade regions. **Crystals** of calcium oxalate are generally absent.

LEAF

Hairs simple, unicellular, sometimes seated on short emergences; glandular types absent. Cells of the **epidermis** often of 2 distinct sizes, the larger ones in some instances projecting as papillae above the leaf surface, e.g. in certain species of *Caylusea*, *Oligomeris*, and *Reseda*. Inner walls of the epidermal cells frequently mucilaginous in species of *Caylusea*, *Ochradenus*, *Oligomeris*, *Reseda*. Mucilaginous cells also recorded in the mesophyll of *Randonia africana* Cosson, and near the leaf veins in *Caylusea*. **Stomata** ranunculaceous, but sometimes accompanied by myrosin cells; recorded as being present on both surfaces in certain species of *Oligomeris* and *Reseda*; those of the xerophyte *Reseda muricata* Presl. not specially protected against excessive transpiration according to Evenari (665). **Mesophyll** not clearly differentiated into palisade and spongy regions, sometimes centric in *Ochradenus* and *Oligomeris*. Vascular bundles of the **veins** not accompanied by mechanical tissue. **Petiole**, in transverse sections, exhibiting a single vascular strand in *Astrocarpus*, but with an arc of bundles in certain species of *Reseda*.

AXIS

YOUNG STEM (Fig. 26 F)

Cells of the **epidermis** becoming sclerosed in old stems of *Ochradenus*. Palisade **chlorenchyma** and **mucilaginous cells** present in the cortex of *Ochradenus baccatus* Del. in which the leaves are reduced. **Myrosin cells**

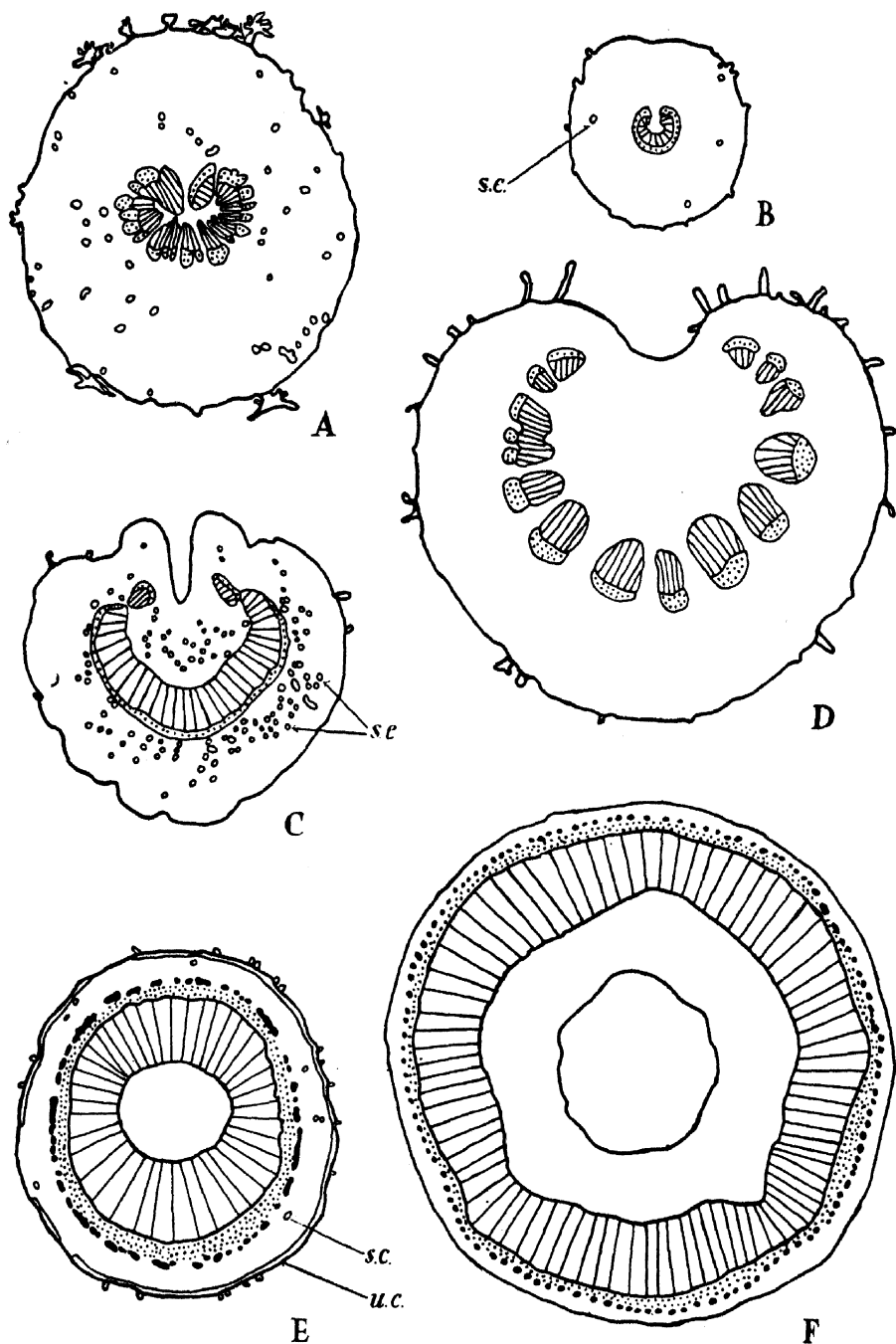


FIG. 26. CAPPARIDACEAE, A-E; RESEDACEAE, F.

A, *Steriphoma ellipticum* (DC.) Spreng. Petiole $\times 25$. B, '*Capparis linearis* Jacq.' Petiole $\times 25$. C, *Crataeva religiosa* Forst. Petiole $\times 25$. D, *Cleome spinosa* Jacq. Petiole $\times 25$. E, '*Capparis linearis* Jacq.' Stem $\times 25$. F, *Reseda luteola* Linn. Stem $\times 8$.
s.c. Secretory canal. u.c. Layer of stone cells with U-shaped thickenings.

exhibiting a red colour when treated with Millon's reagent, and often distinguishable from their neighbours by their greater length, recorded in the stem of *Reseda* spp. **Pericycle** including strands of fibres in *Ochradenus* and *Reseda*. **Xylem** and **phloem** forming closed cylinders traversed by narrow, primary medullary rays. Vessel perforations simple.

WOOD

The secondary xylem is very similar in *Ochradenus* and *Reseda*. **Vessels** with small lumina and simple perforations. **Fibres** with simple pits. **Rays** 1-2 cells wide.

ROOT

Woody or fleshy in different species. Containing **myrosin cells** similar to those in the stem. Primary structure diarch.

ECONOMIC USES

The well-known Mignonette of gardens is *Reseda odorata* Linn.

TAXONOMIC NOTES

The general structure of the stem, as well as the occurrence of myrosin cells, suggests that the Resedaceae have affinities with the Cruciferae. Myrosin cells also occur in some of the Capparidaceae. It is interesting to note that the stomata are not cruciferous.

GENERA DESCRIBED

Astrocarpus,* *Caylusea*, *Ochradenus*, *Oligomeris*, *Randonia*, *Reseda*.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Bolle 221, Evenari (Schwarz) 665.

29. CISTACEAE

(FIG. 27 on p. 98; FIG. 28 on p. 100; FIG. 29 on p. 106)

SUMMARY

(i) GENERAL

A family of woody or somewhat wiry herbs, but also including some shrubs. Many species occur in the Mediterranean region. Most members of the family are especially characterized by the nature of the **hairs**, which are of the following kinds. (i) Simple, unicellular, rigid, appearing, when mature, to have a double structure in their basal portions. (ii) Tufted, each component often similar in structure to the simple hairs of type (i). (iii) Peltate. (iv) Various forms of uniseriate and frequently capitate glands. The **xylem** and **phloem** are in the form of a continuous cylinder around the pith. Calcium oxalate is usually present in the form of abundant cluster **crystals**.

(ii) Wood

Vessels small and numerous, occasionally with a tendency to arrangement in radial or tangential rows or to be semi-ring-porous; numerous; perforations simple, intervacular pitting alternate and small, pits to ray cells similar, members moderately to very short. **Parenchyma** absent or very rare. **Rays** uniseriate in most species, but sometimes up to 3 cells wide, low and heterogeneous. **Fibres** with bordered pits, except in part of 1 genus, extremely short.

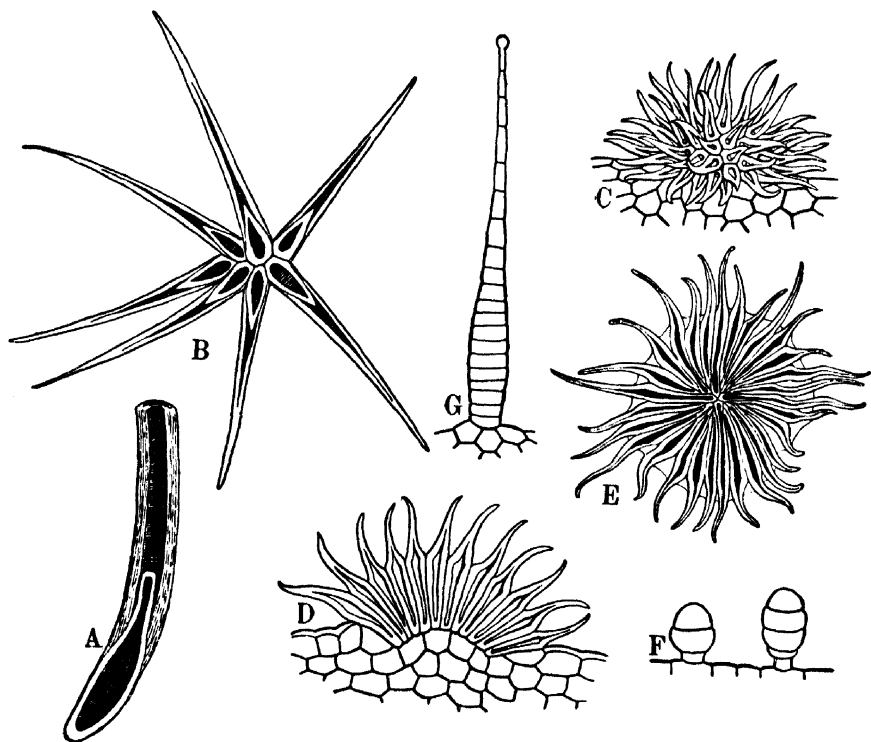


FIG. 27. CISTACEAE

A, Basal part of a simple hair of *Cistus creticus* L. B, Tufted hair of *Cistus creticus* L. C-D, Tufted hairs from the bracts of *Cistus ladaniferus* L. E, Peltate hair of *Helianthemum squamatum* (L.) Pers. F-G, Glandular hairs: F, *Cistus ladaniferus* L.; G, *Cistus creticus* L.—By Solereder.

LEAF

Dorsiventral or centric. **Hairs** of several kinds. (i) Simple, unicellular, rigid hairs which appear, when mature, to have a second hair included in their basal portions (Fig. 27 A-B). The basal portion of these hairs in Fig. 27 A-B, as well as the apparent secondary ones included within them, are stained yellow when treated with eau de Javelle, whilst Schultze's solution shows that the distal part of the outer hair is of cellulose, but that the basal portion of the outer and the whole of the inner hair are lignified. (According to Solereder, whose views are supported by Gard (742), this peculiar structure originates after the young hair has become thickened, when the protoplasm retreats to the base and secretes a cellulose cap which projects acutely towards the apex

of the hair, although it is enclosed within it. Contrary to Solereder's statement, microchemical tests show that the 'cap' of the inner hair is lignified. It seems probable that the mode of development of these hairs would be worth reinvestigating.) (ii) Tufted hairs (Fig. 27 C-D), consisting of several members, each of which is often of the same type as the solitary ones described above, but with their bases sunk in groups in the epidermis. Sometimes individual hairs of a group are relatively short, and their basal portions concrescent. (iii) Peltate hairs (Fig. 27 E) also occur. (iv) Glandular hairs (Fig. 27 F-G), which are uniseriate and sometimes capitate, but of very variable form, several types sometimes occurring in a single species.

According to Gard (742) the nature of the hairs may be of some value in separating species of *Cistus*. Solitary hairs of the 'double' type recorded especially on *Lechea*, to some extent in *Hudsonia*, and sporadically in other genera. Tufted hairs widespread, probably occurring in all genera, but most prevalent in the Cisteae (*sensu* Janchen) although known in *Hudsonia* as well; exhibiting a considerable range of forms in different genera and species. Stellate hairs, peltate scales, and intermediate kinds of structures occur, the scales sometimes giving a silvery appearance to those parts of the plants covered by them, e.g. in *Halimium atriplicifolium* (Lam.) Spach and *Helianthemum squamatum* (L.) Pers. Scales particularly thick-walled in *Cistus ladaniferus* Linn. The downy covering of hairs, present especially in various species of *Fumana*, said by Janchen (1142) to be formed from glands which have lost their secretory function. **Epidermis** composed of cells with curved or straight anticlinal walls; upper epidermal cells large in *Hudsonia tomentosa* Nutt. according to Starr (2188). Epidermis mucilaginous in certain species of *Helianthemum*. **Stomata** present on both surfaces in most species, but apparently absent from the upper side in *Cistus*; ranunculaceous. **Mesophyll** always including well-developed palisade tissue. Vascular bundles of the **veins** not accompanied by sclerenchyma, but in the more xerophyllous species of *Cistus* said by Gard (742) to be embedded in columns of cells with thick cellulose walls, the columns extending from the upper to the lower epidermis and appearing as a white network surrounding green meshes of chlorenchyma in whole leaves when examined by transmitted light. Veins accompanied by mechanical tissue in *Hudsonia ericoides* Linn. **Petiole** of *Cistus*, in transverse sections through the distal end, exhibiting an arc of 3 or more, often about 5, collateral bundles, the one at the centre being larger than the lateral ones; all of them embedded in ground tissue which is frequently lacunar. Petiole of *Helianthemum* supplied by a single arc-shaped bundle embedded in ground tissue with fewer intercellular spaces. A single petiolar strand stated to occur also in *Lechea*. This generic distinction is not absolute. (The leaves of *Cistus* are persistent, and their structure is stated to vary with increase in age. When 2 years old they are, according to Gard (742), always thicker than first-year leaves, owing to an increase in the number of palisade layers and enlargement of the intercellular spaces. The hairy covering is more dense in young leaves, the glandular hairs in particular being more numerous and their secretory function more active.) **Silica bodies**, resembling cystoliths, recorded in the lamina of *Cistus*. Cluster **crystals** of calcium oxalate abundant.

AXIS

YOUNG STEM (Fig. 28 1)

First-formed **cork** arising in the epidermis in *Cistus*, but later-formed phellogens more deeply seated. Cork described by Gard (742) as specially

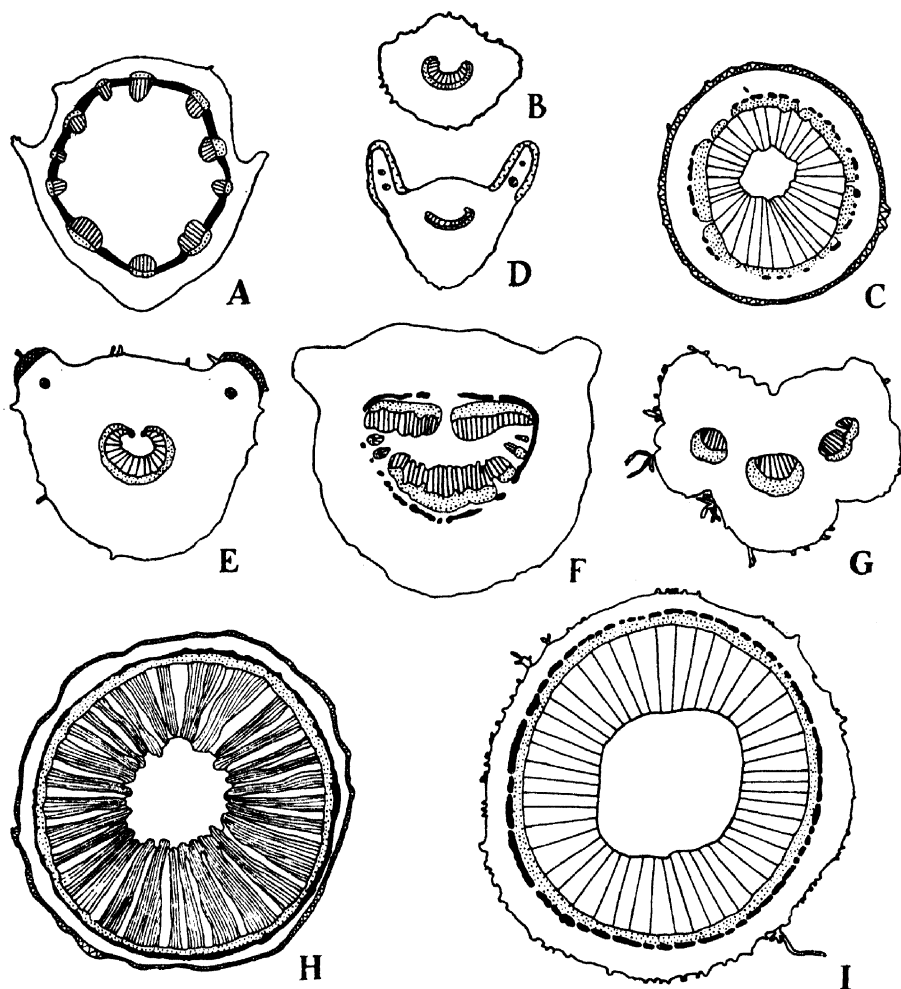


FIG. 28. VIOLACEAE, A-F and H; CISTACEAE, G and I

A, *Viola lutea* Huds. Stem $\times 11$. B, *Hymenanthera obovata* T. Kirk. Petiole $\times 17$. C, *H. obovata* T. Kirk. Stem $\times 17$. D, *Viola lutea* Huds. Petiole $\times 17$. E, *V. odorata* Linn. Petiole $\times 17$. F, *Melicytus ramiflorus* Forst. Petiole $\times 17$. G, *Cistus laurifolius* Linn. Petiole $\times 17$. H, *Melicytus ramiflorus* Forst. Stem $\times 9$. I, *Cistus laurifolius* Linn. Stem $\times 17$.

well developed in desert species of *Helianthemum* belonging to the section *Eriocarpum*. **Cortex** partly sclerenchymatous in *Hudsonia tomentosa* Nutt. according to Starr (2188). Water-storage tissue frequently occurs in the inner part of the cortex, e.g. in *Helianthemum squamatum* (L.) Pers. or in the

endodermal region in *H. apenninum* (L.) Mill. and *H. salicifolium* (L.) Mill. **Endodermis** clearly defined in young stems of certain species of *Helianthemum*, but sometimes less obvious in *Cistus*. **Pericycle** including small strands of thick-walled fibres, apparently more numerous in *Cistus* than in *Helianthemum* in the species examined. **Xylem** and **phloem** present in the form of a closed cylinder surrounding the pith. Vessels small, with simple perforations. Wood fibres with abundant bordered pits. Rays narrow; stated by Solereder to be absent from *Lechea* and according to Janchen (1142) generally from *Hudsonia*. **Pith** fairly broad, consisting of moderately thick-walled pitted cells, many filled with contents which stain deeply with haematoxylin. Contrary to Solereder's statement occasional **canals** with gum-like contents were observed at Kew in the pericyclic region in old stems of a cultivated variety of *Helianthemum*. Cluster **crystals** abundant. Solitary types less frequent.

WOOD¹ (Fig. 29 A and F)

Vessels extremely to very small; exclusively solitary or in occasional pairs; tending to be in radial rows in *Hudsonia* and in tangential rows in *Helianthemum*, section *Eriocarpum*; very numerous, e.g. with more than 100 per sq. mm. in *Cistus*; semi-ring-porous and with spiral thickening in some species of *Cistus*, e.g. in *C. laurifolius* Linn. Perforations simple and oblique. Intervascular pitting alternate and very small; pits to ray cells similar. Solid deposits sometimes abundant in *Cistus*; tyloses rare, except in *Hudsonia*. Mean member length 0.2–0.3 mm. (*Cistus*). **Parenchyma** absent or rare. According to Janchen, absent from *Grocanthemum*, most species of *Fumana*, several species of *Helianthemum* and *Lechea*, but metatracheal parenchyma present in *Cistus*. Vestal, however, states that parenchyma is absent from all these genera and suggests that the low uniseriate rays in some species might easily be mistaken for wood parenchyma. **Rays**, according to Vestal, always present, exclusively uniseriate in *Helianthemum*, *Hudsonia*, and *Lechea* p.p. and 1–3 cells wide in *Cistus* and *Lechea* p.p.; Vestal queries Piccioli's statement, as quoted by Solereder, that rays are absent from *Lechea*; Janchen (1142) states that rays are completely absent from *Hudsonia*, except from *H. montana* Nutt.; very low, usually less than 0.5 mm. high; uniseriates often of only 1–3 cells and composed of mixed procumbent and upright cells; rays very numerous, e.g. 15–25 per mm. in *Cistus*; heterogeneous (Kribs's Types II B and III). **Fibres** with small bordered pits on both radial and tangential walls in *Cistus*, but, according to Janchen, with simple pits in *Helianthemum*, section *Eriocarpum*; walls thin to thick. Mean length about 0.4 mm. in *Cistus*.

TAXONOMIC NOTES

The peculiar nature of the hairs is an interesting and characteristic feature of the family. According to Solereder, hairs with the curious double type of structure are known only in the Combretaceae besides the Cistaceae. Gard (742) has made a special study of the value of anatomical characters in

¹ Based mainly on the descriptions by Janchen (1142) and Vestal (2329).

classifying the species of *Cistus*. His views are well summarized in his own words as follows:

'Nous concluerons que la subdivision des Cistes par les considérations anatomiques ne coïncide pas en tous points avec celle qui a pour fondements les caractères extérieurs. L'anatomie fait apercevoir certaines affinités, certaines liaisons, que n'indique pas la classification des Floristes. Quelle que soit la méthode employée le résultat obtenu n'est pas satisfaisant; et cela parce que certaines espèces ont probablement disparu alors que d'autres sont encore restées inconnues.'

ECONOMIC USES

Labdanum, or Ladanum, a resinous substance used in perfumery, exudes from the leaves and branches of certain species and hybrids of *Cistus*, notably *C. ladaniferus* Linn., *C. villosus* Linn. var. *creticus* (L.) Boiss., and *C. cyprius* Lam. (= *C. ladaniferus* Linn. \times *laurifolius* Linn.). The dried, crushed leaves and young stems of *Cistus* sp. are sometimes used as a substitute for or adulterant of culinary herbs such as Marjoram (*Origanum marjorana* Linn.). *Cistus* leaves have been detected in herb samples submitted to Kew for identification. The characteristic stellate hairs provide an important diagnostic feature.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Cistus,* *Fumana*, *Halimium*,* *Helianthemum*,* *Hudsonia*, *Lechea*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Cistus, (*Crocianthemum*), (*Fumana*), (*Helianthemum*), (*Hudsonia*), (*Lechea*).

LITERATURE

(i) *On General Anatomy*

Gard 742, Janchen 1142, Ponzo 1733, Starr 2188.

(ii) *On Wood Structure*

Janchen 1142, Record 1843, 1851, Vestal 2329.

30. VIOLACEAE

(FIG. 28 on p. 100; FIG. 29 on p. 106)

SUMMARY

(i) GENERAL

Mostly herbs or shrubs, but including a few lianes. The family occurs in temperate and tropical regions. Certain species of *Viola*, especially amongst those from Chile, exhibit unusual habit forms and other ecological specializations such as reduced leaves. The **stomata** are either cruciferous or rubiaceous. The **hairs** are simple and may be unicellular or uniseriate. **Glandular leaf teeth** occur in *Viola*. The **epidermis** is frequently mucilaginous, and some of the cells are frequently filled with brown contents. Calcium oxalate is usually present as solitary or clustered **crystals**. **Inulin** rare. The **stem**, in most of the very limited number of species which have been examined, is

generally characterized by closed cylinders of **xylem** and **phloem**, the former containing a few vessels of small diameter, whilst the phloem is generally devoid of sclerenchyma. In *Viola* some species are provided with closed rings of xylem and phloem, but other members of the genus possess individually distinct bundles, separated from one another by narrow bands of prosenchymatous elements with wide lumina. This difference in organization does not appear to be entirely determined by whether a particular species is woody or herbaceous. In very young stems of *Hymenanchera* the bundles are sometimes just sufficiently separated to be individually distinct, but with increase in age the xylem and phloem form almost completely closed rings. Sclerenchyma is frequently present in groups or almost continuous bands in the **pericycle**, although certain species of *Viola* are devoid of mechanical elements in this region. The **pith** is generally solid in woody species, but frequently becomes hollow in herbs.

(ii) Wood

Vessels small and numerous, occasionally with a radial pattern, sometimes semi-ring-porous and with spiral thickening, perforation plates simple, scalariform, or both, intervacular pitting usually opposite or scalariform, but sometimes alternate, pits to ray cells similar and often simple; members usually of medium length, sometimes very long. **Parenchyma** absent or as rare cells about the vessels. **Rays** absent from *Viola*; in the other genera of 2 distinct sizes, the larger up to 4–10 cells wide; high; often composed entirely of square and upright cells. **Fibres** with simple or bordered pits, septate; usually short to medium, sometimes very long.

LEAF

Generally dorsiventral, but centric in certain species of *Hybanthus*. **Hairs** consisting exclusively of simple unicellular or uniseriate trichomes, apart from the glandular shaggy hairs of the leaf teeth in *Viola*. The latter stated sometimes to secrete lime. **Cuticle** usually thin, sometimes striated. The surface is provided with a thin coating of wax in certain species of *Viola*. **Epidermis** with the inner walls of the cells frequently mucilaginous in certain species of *Leonia*, *Rinorea*, and *Viola* (but not in Hawaiian species of this genus examined by Skottsberg, 2123); mucilaginous cells sometimes appearing as transparent dots in the leaf. Cells containing a reddish, or, more rarely, yellow gum-resin present in the epidermis of certain species of *Agatea*, *Anchietea*, *Corynostylis*, *Isodendron*, *Paypayrola*, and *Viola*; practically the whole epidermis consisting of cells of this kind in some species, but only occasional cells of this kind present in others. (See also under 'Secretory Elements'.) Some of the epidermal cells of *V. mauensis* Mann. considerably larger than their neighbours and serving for water-storage according to Skottsberg (2123). Similar cells not observed by the same author in *V. robusta* Hillebr. but tending to be formed in *V. luciae* Skottsberg, the last species being a hybrid between the first two.

A **hypoderm** of several layers present in *Hymenanchera latifolia* Endl. **Stomata** distinctly cruciferous in *Hybanthus*, *Leonia*, *Paypayrola*, *Rinorea* (pro parte); indistinctly cruciferous in *Amphirrhox*, *Hymenanchera*, *Rinorea* (pro parte); rubiaceous in certain species of *Anchietea*, *Corynostylis*, *Noisetia*,

Isodendron, *Melicytus*; transitional between cruciferous and rubiaceous in certain species of *Hybanthus* and *Viola*. Stomata present on both surfaces or confined to the lower side; confined to the upper surface in *Viola tridentata* Menz. and *V. muscoides* Philippi.; either deeply sunk or in the same plane as the epidermis itself; situated at the bases of small pits or canals in some species of *Viola*. **Mesophyll** including no clearly defined palisade tissue in certain species of *Viola*, but clearly differentiated into palisade and spongy portions in the Hawaiian species of *Viola* examined by Skottsberg (2123). A projecting network, consisting of strands of tissue containing 2-3 layers of palisade cells, recorded by Solereder on the upper surface of an undetermined species of *Viola* from Peru. Arm-palisade cells stated by Sabnis (1977) to occur on the abaxial side in *Viola stocksii* Boiss. Small **vascular bundles** generally not accompanied by sclerenchyma in most herbaceous and certain woody species, but accompanied by sclerenchyma strands or sheaths in certain species of *Melicytus*, *Paypayrola*, and *Rinorea*. Midrib of smaller leaves with only 1 vascular bundle, but 2 present in the larger leaves, the upper bundle having the xylem and phloem inversely orientated; more complex vascular arrangements also occur in large leaves. **Petiole**, in transverse sections through the distal end, exhibiting a single large, crescentic, collateral vascular strand in *Hymenanthera obovata* Kirk (Fig. 28 B); with a single crescent-shaped strand either alone or accompanied by smaller lateral ones in the limited number of *Viola* spp. (Fig. 28 D and E) so far investigated. Transverse sections through the distal end of a petiole of *Melicytus ramiflorus* Forst. (Fig. 28 F) recently examined at Kew showed an almost closed vascular cylinder, flattened and slightly open on the adaxial side, the abaxial part of the cylinder tending to be dissected into separate bundles, the whole vascular strand being surrounded by an interrupted ring of fibres with wide lumina.

Calcium oxalate present as solitary and clustered **crystals** in the mesophyll and petiolar ground tissue. (The existence of 8 types of crystal structure and distribution is recorded by Solereder (2158) and Melchior (1483), but this appears to need reinvestigation. The taxonomic significance of these types also needs to be reassessed because some of the genera in which they are stated to occur are probably members of the Ochnaceae rather than of the Violaceae.) Sphaerocrystalline masses of an organic substance of unknown composition recorded in certain species of *Agatea* and *Rinorea*. **Secretory elements**. Skottsberg (2123) records the occurrence of secretory cells with brown contents in the mesophyll but not in the epidermis of the Hawaiian plants *Viola luciae* Skottsb. and *V. mauianensis* Mann., but none seen in *V. robusta* Hillebr. The old stipules in the same species wholly composed of these cells. (See also under 'Epidermis' above.) Various kinds of **ecological specializations**, which are believed to reduce transpiration, occur in *Viola*, notably in the sections *Andinium* and *Tridens*.

AXIS

YOUNG STEM (Fig. 28 A, C, and H)

Epidermis composed of tabular cells with thick outer walls, but locally elongated in a palisade-like manner in *Viola stocksii* Boiss. according to Sabnis (1977). Epidermal cells, oval with thin walls in *V. cunninghamii* Hook. f.; large, rectangular with thin walls in *Hymenanthera dentata* R.Br. var.

alpina Kirk.; inner walls gelatinized in the Hawaiian species of *Viola* examined by Skottsberg (2123). A **hypoderm** of large thin-walled cells noted at Kew in *Melicytus ramiflorus* Forst. **Cork** described by Betts (188) as having the form of a wide band in *Hymenanchera dentata*. Seen to arise superficially in *Hymenanchera obovata* Kirk. and *Melicytus ramiflorus*; component cells with greatly thickened inner tangential walls in the last species. **Cortex** collenchymatous in *Viola stocksii* according to Sabnis (1977); parenchymatous in *V. cunninghamii* (Betts 188); consisting of thick-walled cells containing **oil drops** in *Hymenanchera dentata*. **Endodermis** described by Betts (188) as well defined, and consisting of large cells with thin suberized walls in *Viola cunninghamii*. **Pericycle** including strands of fibres, in *Amphirrhox*, *Hybanthus*, *Hymenanchera*, *Melicytus*, *Paypayrola*, and *Rinorea*, the strands often becoming connected by stone cells to appear as a complete ring in transverse sections. Sclerenchyma said by Sabnis (1977) to be absent from the pericycle in *Viola stocksii* and by Betts (188) from *V. cunninghamii*. **Phloem** according to the last 2 authors forming a closed ring in *Hymenanchera dentata*, *Viola cunninghamii*, and *V. stocksii*. **Xylem** constituting a closed ring with very few vessels in *Hymenanchera dentata* according to Betts (188). The existence of this structure also observed by the same author in other species of *Hymenanchera* as well as in *Viola cunninghamii*. Primary vascular bundles of *Melicytus ramiflorus* Forst. (Fig. 28 H) examined at Kew appeared individually distinct in transverse section, but united by lignified medullary ray tissue. Vessels in the secondary xylem of slightly older stems of the same species mostly in radial multiples, but a few solitary and in irregular clusters. Vascular bundles also individually distinct and separated from one another by narrow bands of prosenchymatous elements with wide lumina in certain species of *Viola* (Fig. 28 A). Vessels with simple perforations and some scalariform plates (see 'Wood'). **Pith** generally solid in woody, but sometimes becoming hollow in herbaceous species; the cells sometimes containing brown deposits in woody species. Pith composed of moderately thick-walled pitted cells in *Melicytus ramiflorus*. Solitary and clustered **crystals** often abundant.

Skottsberg (2123) has recently recorded the following additional information concerning the stem structure of the **Hawaiian species** *Viola robusta* Hillebr., *V. mauensis* Mann., and *V. luciae* Skotts., the last being a hybrid between the first 2 species. Amongst the characters noted in old stems of *V. robusta* were the following. Primary cortex well developed. Endodermis not clearly differentiated. Pericycle containing starch. Secondary phloem in the form of a cylinder. Xylem dense, all constituent elements more or less rectangular in transverse sections. No medullary rays visible in longitudinal sections, but radiating rows of cells devoid of vessels observed in transverse sections. Vessels narrow, infrequent, some of those near the primary xylem provided with more or less well-defined scalariform perforation plates. Occasional solitary vessels with brown contents noted. Short rectangular cells with thick, lignified, pitted walls present between the protoxylem strands and also forming a cylinder around the pith. Pith solid, even in the thickest stems, but sometimes ruptured in dried material; composed of large, thin-walled, amyloiferous, parenchymatous cells. Cluster crystals present in the cortex and pith. Stem of *V. mauensis* similar in structure, but phloem

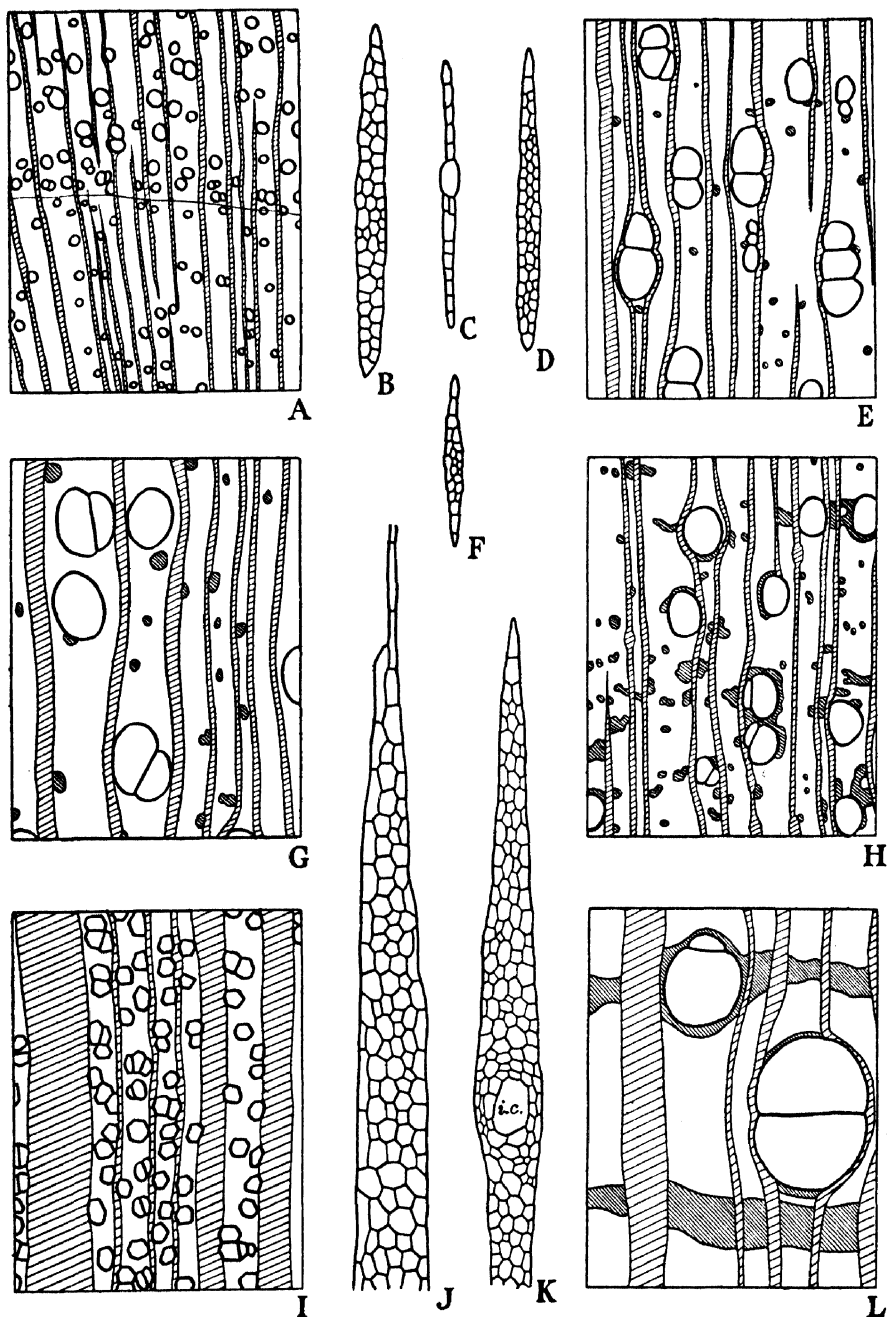


FIG. 29. CISTACEAE, A and F; CANELLACEAE, B-C and G-H; BIXACEAE, D-E; VIOLACEAE, I-J; COCHLOSPERMACEAE, K-L

A, *Cistus laurifolius* Linn. B, *Warburgia ugandensis* Sprague. C, *Cinnamosma fragrans* Baill. Showing oil cell. D, *Bixa orellana* Linn. E, *B. orellana* Linn. F, *Cistus laurifolius* Linn. G, *Warburgia ugandensis* Sprague. H, *Cinnamosma fragrans* Baill. I, *Amphirrhox longifolia* Spreng. J, *A. longifolia* Spreng. K, *Cochlospermum orinocoense* Steud. L, *C. williamsii* Macbride.
i.c. = intercellular canal.

containing numerous brown cells, and a circle of similar cells in the wood parenchyma. Characters of the hybrid *V. luciae* intermediate between those of the parents.

WOOD (Fig. 29 i and j)

Vessels usually very small (mean tangential diameter 25–50 μ), but occasionally medium-sized (100–200 μ), e.g. in *Agatea violaris* A. Gray; exclusively solitary in *Agatea violaris* and *Anchietia* (1886) and almost so in *Viola chamissoniana* Gilg.; solitary and in short radial multiples in the other genera and occasionally in radial rows, e.g. in *Hybanthus* (1886) and *Paypayrola longifolia* Tul.; usually about 25–70 per sq. mm.; very few, according to Betts (188), in *Hymenanchera dentata* R.Br. var. *alpina* Kirk.; with spiral thickening in *Hybanthus* and *Hymenanchera*; semi-ring-porous in *Hymenanchera*. Perforation plates usually exclusively simple in *Agatea*, *Anchietia* (1886), *Hybanthus*, *Hymenanchera*, *Melicytus*, and *Viola*, and exclusively scalariform in *Alsodeia* p.p. (2158), *Amphirrhox*, *Gloeospermum*, *Leonia*, *Paypayrola*, and *Rinorea*, but Solereder lists the following as having both simple and scalariform plates: *Anchietea*, *Alsodeia* p.p., *Corynostylis*, *Hymenanchera*, *Ionidium* and *Noisetia*; Janssonius (1154) notes a few simple perforations in *Alsodeia cymulosa* Miq.; the scalariform plates with few to numerous bars and sometimes accompanied by irregular, coarsely reticulate plates. Intervascular pitting typically alternate to opposite, but scalariform in *Paypayrola* and sometimes in *Leonia* (1886); the pits usually moderate-sized to rather large, but very small in *Hybanthus* and *Melicytus*; pits to ray cells similar to the intervacular pitting or larger, often simple or with very narrow borders. Pitted tyloses sometimes present, e.g. in *Agatea* and *Amphirrhox*. Mean member length 0.4–0.9 mm., but as much as 1.3 mm. in *Paypayrola* (1283). **Parenchyma** absent or extremely sparse; when present, paratracheal, as a few cells about the vessels; Dadswell and Record (533), however, describe the parenchyma as 'sparingly paratracheal or diffuse' and Williams (2430) refers to fine lines between the rays in *Leonia glycyarpa* Ruiz. et Pav. **Rays** absent from *Viola*; in the other genera of 2 distinct sizes, the larger up to 4–10 cells wide and often more than 3 mm. high; reported to be wholly uniseriate or only partially biseriate, in *Gloeospermum sprucei* Eichl. (2430) and in *Hymenanchera dentata* var. *alpina* (188); uniseriates numerous and composed of upright cells; usually about 12–15 rays per mm.; the large rays usually composed almost entirely of square to upright cells, with uniseriate marginal rows of 4–10, or sometimes more, cells; often with a tendency to sheath cells (Fig. 29 j); commonly containing numerous single crystals. Perforated ray cells sometimes present (358). **Fibres** septate and with simple or indistinctly bordered pits in most genera, but with small bordered pits in *Agatea* and *Viola* and, according to Solereder, with both simple and bordered pits in *Anchietea* and *Corynostylis*. Walls thick, often with a gelatinous layer. Mean length usually 0.5–1.2 mm. (100), but up to 2.5 mm. in *Paypayrola* (Martin-Lavigne, 1450).

PEDUNCLE

The following features have been recorded by Skottsberg (2123) concerning the Hawaiian species of *Viola* which he examined. Transverse sections of

Viola robusta Hillebr. show 4 wide vascular bundles separated by medullary rays. Secondary tissues probably not formed in this species. Structure in *V. mauensis* Mann. differing somewhat from that of *V. robusta* as follows. Epidermis and sub-epidermis composed of cells with thickened, gelatinized walls. Secondary xylem in the form of a closed cylinder with numerous strands of primary xylem on the inside. Secretory cells with brown contents in the cortex, and with yellowish contents in the phloem. Transverse sections of thick specimens of the scape of the herbaceous *V. kauaiensis* Asa Gray exhibit considerable development of secondary xylem and medullary rays with lignified cell walls. Numerous cluster crystals in the cortex and pith of this species.

ROOT

Inulin stated by Solereder to be present in *Hybanthus* (*Ionidium*) *ipecacuanha* (L.) Baill.

TAXONOMIC NOTES

Further investigation, especially of the woody members of this family, seems to be desirable in order that its affinities may be more definitely established. The genera *Lavradia*, *Schuurmansia*, and *Sauvagesia*, which were included by Bentham and Hooker in the Violaceae-Sauvagesiae, are described in this book under the Ochnaceae, where they have been included by Gilg (770) and Hutchinson (1113). They differ anatomically in certain important respects from the Violaceae.

Taylor (2237) has drawn attention to the similarity in wood anatomy between this family and the Flacourtiaceae, and has suggested that the Turneraceae may also belong to this complex. Taylor also points out that, although placed high in the Archichlamydeae, these families exhibit many primitive features in their wood anatomy.

ECONOMIC USES

The root of *Hybanthus* (*Ionidium*) *ipecacuanha* (L.) Baill. is used as a substitute for true *Ipecacuanha* root (*Cephaelis ipecacuanha* (Brot.) A. Rich) family Rubiaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Agatea, Amphirrhox, Anchietea, Corynostylis, Hybanthus, Hymenanthera,* Isodendron, Leonia, Melicytus,* Noisettia, Paypayrola, Rinorea, Viola.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Agatea, (Alsodeia), Amphirrhox, (Anchietea), (Corynostylis), Gloeospermum, Hybanthus, Hymenanthera, (Ionidium), Leonia, Melicytus, (Noisettia), Paypayrola, Rinorea, Viola.

LITERATURE

(i) *On General Anatomy*

Betts 188, Gilg 770, Hutchinson 1113, Melchior 1483, Meyer 1504, Sabnis 1977, Sayeedud-Din 2012, Skottsberg 2123, Thompson, W. P. 2254.

(ii) *On Wood Structure*

Bailey 100, den Berger 182, Betts 188, Chalk and Chattaway 358, Dadswell and Record 533, Janssonius 1154, Kribs 1283, Martin-Lavigne 1450, Pfeiffer, J. Ph. 1713, Record 1843, 1851, Record and Hess 1886, Taylor 2237, Thompson 2254, Williams, Ll. 2426, 2430.

31. CANELLACEAE

(FIG. 29 on p. 106; FIG. 30 on p. 118)

SUMMARY

(i) GENERAL

Glabrous, aromatic trees, from tropical America, E. Africa, and Madagascar, which are characterized especially by the presence of **secretory cells** in the parenchyma of the axis and leaf as well as in the wood. The **stomata** are generally rubiaceous, although no definite subsidiary cells are present in *Cinnamosma fragrans* Baill. Bundles of fibres usually occur in the **pericycle**, although they are sometimes rather late in developing. A well-developed **phelloderm** is generally formed. Calcium oxalate is most often secreted in the form of clustered **crystals**, although solitary ones occur as well. The **medullary rays** are narrow in the wood but broaden considerably in the phloem.

(ii) WOOD

Vessels small, solitary, and few, perforation plates scalariform, intervacular pitting opposite or occasionally elongated, members very to extremely long. **Parenchyma** diffuse, or about the vessels, or both; containing numerous oil or mucilage cells. **Rays** wholly uniseriate or up to 3 or 4 cells wide, homogeneous or nearly so, or of square and upright cells only, oil or mucilage cells absent from most species. **Fibres** with conspicuous bordered pits, moderately to very long.

LEAF

Epidermis with straight anticlinal walls. **Stomata** confined to the lower surface; rubiaceous in *Canella* and *Cinnamodendron*, but ranunculaceous in *Cinnamosma fragrans* Baill. A single layer of **hypoderm** also occurs in *C. fragrans*. **Mesophyll** said by Solereder to include no palisade tissue in species of *Canella* and *Cinnamodendron* hitherto examined. Vascular bundles of the **veins** accompanied above and below by strands of fibres. Midrib including a single vascular bundle. **Petiole** stated to exhibit 3 vascular bundles accompanied by sclerenchyma in *Cinnamosma*; a single, very open, arc-shaped strand containing radial groups of small vessels in the xylem observed at Kew in transverse sections through the distal end in *Canella alba* Murray (Fig. 30 H). Vascular strand in the last species accompanied by rather scanty sclerenchyma. **Secretory cells** with yellow contents always present, appearing as transparent dots in cut leaves. Calcium oxalate usually secreted in the form of clustered

crystals, -but small solitary crystals sometimes present as well. Small crystals situated in the epidermis of *Canella*.

AXIS

YOUNG STEM (Fig. 30 K)

Cork originating in the sub-epidermis in *Canella* and *Cinnamodendron*. A layer of phelloderm present in older stems, the inner cell walls being provided with U-shaped thickenings in *Canella*. **Pericycle** containing bundles or a continuous ring of fibres in *Canella* and *Cinnamosma*; pericyclic sclerenchyma stated to be absent from *Cinnamodendron*. The amount of sclerenchyma appears to vary with age in *Canella* and probably in the other genera as well. **Phloem** characterized by sieve-tubes with scalariform sieve-plates. **Xylem** constituting a closed cylinder traversed by narrow rays. Vessels with scalariform perforation plates. **Secretory cells**, similar to those in the leaf, present in the cortex and xylem.

WOOD (Fig. 29 B-C and G-H)

Vessels moderately small (mean tangential diameter 50-100 μ) or slightly larger; usually exclusively solitary, apart from apparent tangential or oblique pairs due to overlapping ends; sometimes with a few radial pairs in *Warburgia* and occasionally in short radial rows of vessels, which, however, are not in actual contact (1886); usually about 4-10 per sq. mm., but more numerous in *Capsicodendron*. Perforation plates exclusively scalariform, with 10-60 bars (2329). Intervascular pitting rare, opposite, moderately large to large, sometimes horizontally elongated; pits to ray cells similar to the intervacular pitting. Mean member length 1.2-2.3 mm. **Parenchyma** apotracheal in *Capsicodendron* and *Warburgia*, as isolated cells scattered among the fibres and in short tangential lines (Fig. 29 G); paratracheal in *Canella* and *Pleodendron*, rather scanty and limited to the abaxial sides of the pores; both types present in *Cinnamosma*, the paratracheal parenchyma often vasicentric (Fig. 29 H). Strands commonly of 12-16 cells. Oil or mucilage cells present in *Canella*, *Capsicodendron*, *Cinnamosma*, and *Warburgia*. **Rays** 1 (occasionally 2) cell wide in *Canella*, *Capsicodendron*, *Cinnamosma*, and *Pleodendron*, commonly 2-3 (up to 4) cells wide in *Warburgia*; usually low, but occasionally 1 mm. high in *Canella* and *Warburgia*; uniseriates moderately numerous in *Warburgia* and composed of cells similar to those of the multi-seriate rays; about 10-15 rays per mm.; homogeneous (Kribs's Type I), with only occasional marginal rows of square cells, e.g. in *Warburgia*, or composed almost entirely of square to upright cells, e.g. in *Cinnamosma*; commonly containing crystals. Oil or mucilage cells in the rays observed only in *Cinnamosma* (Fig. 29 c). **Fibres** with numerous, conspicuously bordered pits, equally numerous on both radial and tangential walls and of about the same size as the intervacular pitting. Walls moderately thin to thick. Mean length 1.5-2.7 mm.

TAXONOMIC NOTES

Vestal (2329) in a study of the wood anatomy of the Guttiferae and their allies, concludes that the Canellaceae do not belong to this group of families and suggests that they could well be placed near the Myristicaceae and the

arboreal Ranales. Garratt, on the other hand, in a study of the woods of the Myristicaceae (747), concludes that, despite certain points of similarity, the Canellaceae seem rather far removed from this family. In another study (747 A) Garratt concludes that, on the basis of wood anatomy, no relationship with the Monimiaceae can be inferred.

The most outstanding feature of the wood, the oil or mucilage cells of the rays and wood parenchyma, suggests affinity with the Magnoliaceae and the Lauraceae. Though other characters lend little direct support, most of the points of difference between the Canellaceae and the Lauraceae, except for the common occurrence of septate fibres in the latter, might be explained as due to different levels of specialization. Vessel member length and some other characters suggest that the Canellaceae are much less highly specialized than the Lauraceae and are even less specialized than the Magnoliaceae. Affinity with the Lauraceae would imply relationship to the Monimiaceae and Hernandiaceae, all of which have anatomical features in common.

ECONOMIC USES

The bark of *Canella alba* Murray is used for medicinal purposes. The bark of this species is characterized by phelloderm consisting of stone cells strongly thickened on the radial and inner walls; numerous oil cells; starch grains simple or 2-3 compound, individual grains being up to 20 (usually 5-10) μ in diameter; cluster crystals of calcium oxalate; fibres occasionally present in the pericycle but absent from the phloem. The scented wood of *Cinnamosma fragrans* Baill. is exported from Zanzibar to Bombay, and probably Siam, where it is used in religious ceremonies. Further details concerning this wood have been recorded by Metcalfe (1496).

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Canella,* Cinnamodendron, Cinnamosma.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Canella, (Capsicodendron), Cinnamosma, (Pleodendron), Warburgia.

LITERATURE

(i) On General Anatomy

Gilg 772, Greenish and Wallis 812.

(ii) On Wood Structure

Garratt 747, 747 A, Howard 1088, Kanehira 1209, Record 1783, 1790, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Metcalfe 1496, 1497, Vestal 2329.

32. BIXACEAE

(FIG. 29 on p. 106; FIG. 30 on p. 118)

SUMMARY

A small tropical family consisting of the single genus *Bixa*. Owing to the somewhat conflicting statements in the literature, the following description of the leaf and young stem of the small tree *Bixa orellana* Linn. has been based mainly on original observations on material grown at Kew. The wood exhibits the following features. **Vessels** moderately small, with numerous small multiples, perforations simple, intervascular pitting alternate and minute, pits to parenchyma similar, members moderately short. **Parenchyma** diffuse, storied. **Rays** mostly 1–3 cells wide, heterogeneous, the uniseriates storied. **Fibres** with bordered pits, storied, moderately short.

LEAF

Dorsiventral. **Hairs** described by de Boer (214) as either tufted or peltate, the former consisting of small groups of unicellular trichomes and the latter of a circular disk supported by a short quadricellular base. **Stomata** confined to the lower surface; ranunculaceous; about 115 per sq. mm. **Petiole** (Fig. 30 G) almost circular in transverse section. Blocks of sclerenchyma, appearing as an almost continuous ring because so closely packed together, present immediately on the outside of the petiolar vascular strand, the latter, in transverse sections through the distal end of the petiole, appearing to consist of an almost continuous ring of phloem situated externally to a more interrupted ring of xylem. Enclosed within the vascular ring is a central mass of parenchyma with a subsidiary, collateral vascular strand, unaccompanied by sclerenchyma, embedded in it. Xylem of the central strand appearing as 2 separate groups at least in some sections. **Secretory canals**, surrounded by an epithelium of small cells and filled with dark refractive contents, situated in the parenchymatous portion of the petiole both within and external to the main vascular ring. **Secretory cells** present in the mesophyll and in the peripheral tissues of the petiole. Cluster **crystals** of calcium oxalate abundant.

AXIS

YOUNG STEM (Fig. 30 J)

Cork superficial in origin. **Pericycle** including an almost continuous or somewhat interrupted, composite ring of sclerenchyma. **Phloem** appearing in transverse sections as strands separated from one another by the triangular distal ends of the medullary rays, the widest portion of each ray being in contact with the pericyclic sclerenchyma. Phloem stratified into alternating hard and soft zones by approximately concentric rings of strands of fibres. **Xylem** in the form of a closed cylinder traversed by narrow rays. **Secretory canals** present in the pith; and **secretory cells** in the outer part of the cortex. Cluster **crystals** of calcium oxalate occur in the cortex and pith.

WOOD (Fig. 29 D–E)

Vessels moderately small to medium-sized (mean tangential diameter 90μ in material examined); solitary and in numerous radial multiples of 2 or 3 cells;

about 20 per sq. mm. in material examined. Perforations simple, transverse to oblique. Intervascular pitting alternate, minute and crowded. Pits to ray cells similar to the intervacular pitting. Mean member length about 0.3 mm. **Parenchyma** apotracheal, as scattered cells (Fig. 29 E) and short lines from ray to ray. Strands usually of 4 cells. Storied. **Rays** up to 3, occasionally 4, cells wide; mostly low, but the multiseriate rays sometimes up to 1 mm., and commonly 2-3 stories, high; uniseriates moderately numerous and composed of upright, square, and procumbent cells; about 11 rays per mm.; heterogeneous (Kribs's Type II B), the multiseriate rays usually with not more than 1 or 2 marginal rows of upright cells. Uniseriate rays storied. **Fibres** with rather few, small, bordered pits on both radial and tangential walls, the borders slightly larger than those of the intervacular pits. Storied. Mean length about 0.8 mm.

TAXONOMIC NOTES

The stratification of the phloem into hard and soft portions, the broadening of the rays where they traverse the phloem, and the complex vascular structure of the petiole all suggest that *Bixa* has affinities with the Cochlospermaceae and Tiliaceae. The anatomy of the wood is in agreement with this view, and the absence of septate fibres and the presence of diffuse parenchyma distinguish the wood of *Bixa* very clearly from the woods of the Flacourtiaceae. Secretary canals are also to be found at least in certain members of all these families. The classification of *Bixa* and certain genera, now included in the Flacourtiaceae, together in one family as in the system of Bentham and Hooker presents difficulties on other anatomical grounds, besides the differences in wood structure just mentioned above. Solereder (2158) evidently appreciated this difficulty also, because he begins his account of the Bixaceae as understood by Bentham and Hooker by remarking that 'Anatomical characters common to all members are almost entirely wanting in the Order'.

ECONOMIC USES

The seeds of *Bixa orellana* Linn. yield Annatto dye which is not very durable. It is used for colouring butter and cheese, &c.

GENUS DESCRIBED

Bixa.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, de Boer 214, Pilger 1722.

(ii) *On Wood Structure*

Record 1809, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2206, Vestal 2329.

33. COCHLOSPERMACEAE

(FIG. 29 on p. 106)

SUMMARY

(i) GENERAL

The anatomy of the small tropical trees and shrubs included in this family needs further investigation. Some of the following facts concerning the leaf and young stem have been taken from Pilger's (1723) account.

(ii) WOOD

Vessels medium-sized to large and rather few, perforations simple, intervascular pitting alternate and rather large, pits to parenchyma often large and simple, members of medium length. **Parenchyma** mostly as broad apotracheal bands, but also vasicentric, storied. **Rays** up to 5 or 6 cells wide, uniseriate common and storied, multiseriate 2 or more stories high, heterogeneous. **Fibres** with small bordered pits, often storied, of medium length. Radial **intercellular canals** usually present.

LEAF

Hairs mostly long, simple, unicellular, but peltate forms also occur in *Cochlospermum*. **Epidermis** often composed of mucilaginous cells. **Stomata** confined to the lower surface in *Amoreuxia* and *Cochlospermum* but recorded on both sides in *Sphaerosepalum alternifolium* Bak. Vascular bundles of the smaller **veins** not accompanied by sclerenchyma. **Petiole** with 3 bundles entering the base in *Amoreuxia*, *Cochlospermum*, and *Sphaerosepalum*, but exhibiting a closed cylindrical strand in transverse sections through the distal end. Subsidiary, medullary bundles such as those in *Bixa* (Family Bixaceae) absent from the petiole. **Secretory cells** with yellow or reddish resinous contents present in the mesophyll of *Amoreuxia* and *Cochlospermum*; large mucilage cells recorded in the corresponding position in *Sphaerosepalum*. Large prismatic **crystals** also present in the mesophyll of *Sphaerosepalum*.

AXIS

YOUNG STEM

Pericycle including isolated strands of fibres. **Phloem** traversed by the triangular distal ends of the medullary rays as in some of the Bixaceae and Tiliaceae; stratified into sclerosed and soft portions in *Cochlospermum*. **Secretory cells** with yellow or reddish resinous contents recorded in the primary cortex of *Amoreuxia* and *Cochlospermum*, and large mucilage cells in the corresponding position in *Sphaerosepalum*. **Mucilage canals** present in the inner part of the cortex and the periphery of the pith in *Amoreuxia* and *Cochlospermum*. Large prismatic **crystals** present in the primary cortex of *Sphaerosepalum*.

WOOD (Fig. 29 K-L)

Vessels medium-sized (100–200 μ mean tangential diameter) to large (more than 200 μ); solitary and in small multiples; about 5–7 per sq. mm. Perforations simple. Intervascular pitting alternate, rather large and often

with horizontal apertures; pits to ray and wood parenchyma usually larger than the intervacular pits, elongated horizontally and simple. Tyloses sometimes abundant. Mean member length about 0.6 mm. **Parenchyma** predominantly apotracheal; in regular to irregular bands 2–8 cells wide and in narrow sheaths about the vessels (vasicentric) (Fig. 29 L). Strands usually of 4 cells. Storied. Cell walls very thin and apparently unglified; the cells of the bands sometimes much dilated, e.g. in *Cochlospermum vitifolium* (Willd.) Spreng. Strands usually of 4 cells. **Rays** typically up to 5 or 6 cells wide, but with occasional very wide and high rays in some species; uniseriate moderately numerous, composed of both procumbent and upright cells and often storied; multi-seriate rays usually 2 or more stories high; about 6 rays per mm.; heterogeneous (Kribs's Type II B) with 1–2 marginal rows of square to upright cells. **Fibres**. Pits with very small borders, mostly on the radial walls. Walls moderately to very thin. Often storied and sometimes markedly 'bauchig'. Mean length about 1.1 mm. **Intercellular canals** usually present in some of the rays, but not common (Fig. 29 K).

TAXONOMIC NOTES

Amoreuxia and *Cochlospermum* have characters in common with the Bixaceae as understood in the systems of Engler and Prantl and Hutchinson. In Dr. Hutchinson's opinion, however, *Sphaerosepalum* should not be included in the Cochlospermaceae, its affinities appearing to lie rather with the Guttiferae. It will be seen above that there are anatomical differences between *Sphaerosepalum* and the two other genera, but *Sphaerosepalum* needs further anatomical investigation before an opinion on its taxonomic position can be expressed by an anatomist.

ECONOMIC USES

Cochlospermum gossypium DC. from India yields Katira Gum. A yellow dye is obtained from the roots of *Cochlospermum tinctorium* Rich.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Amoreuxia, *Cochlospermum*, *Sphaerosepalum*.

(ii) FOR WOOD STRUCTURE

Cochlospermum.

LITERATURE

(i) *On General Anatomy*

Pilger 1723.

(ii) *On Wood Structure*

Record 1851, Record and Hess 1886, Vestal 2329, Williams 2430.

34. FLACOURTIACEAE

(FIG. 30 on p. 118; FIG. 31 on p. 120)

SUMMARY

(i) GENERAL

A family of woody plants which are mostly shrubs or small trees; occasionally they attain a considerable size. The family is mostly tropical, although a few genera are known from South Africa, New South Wales, Chile, whilst *Idesia* grows in Japan. The anatomy does not exhibit any particularly striking or noteworthy features, but a more complete examination might well be undertaken, as many of the genera do not appear to have been investigated. **Hairs.** Simple, unicellular, sclerenchymatous trichomes; tufted; 2-armed; stellate; peltate; uniseriate, with thin partitions between the component cells. The **stomata** are rubiaceous or cruciferous. The **petiole**, in the few species investigated, is provided at the distal end with either 1 vascular bundle or with 3 which may become united to form an arc which is open on the adaxial side. Schizogenous **secretory cavities** occur in many of the genera which were included by Bentham and Hooker in the Samydaceae. Calcium oxalate is present as clustered or solitary **crystals**, sometimes situated in specialized cells (crystal-idioblasts) in the epidermis. The nature and distribution of the calcium oxalate crystals is often helpful in recognizing genera and species. The presence of large solitary prisms in some of the stone cells of the pericycle of the young stem is characteristic of certain genera, whilst in others there is an abundance of cluster crystals in the phloem. Cluster crystals were also found to be very numerous in the parenchymatous tissues of the petiole in all of the species available for examination. Further details are recorded under 'Axis'.

The **pericycle** in the young stem includes strands of fibres which are sometimes united by stone cells to form a composite ring, which in some genera is rather broad. The **phloem** is not stratified into hard and soft portions, and the medullary rays are not known to be broadened where they traverse the phloem except in *Erythrospermum*. The phloem and xylem in young stems are in the form of closed cylinders traversed by narrow rays.

(ii) WOOD

Vessels usually moderately small; solitary and in twos and threes; occasionally with spiral thickening, perforations usually all simple, but some genera with a few, and others with wholly, scalariform plates; intervascular pitting (a) scalariform, opposite or large and alternate, with pitting to ray cells large and often scalariform, or (b) very small and alternate, with pits to ray cells similar; members moderately to very long. **Parenchyma** absent or very sparse; when present paratracheal. **Rays** usually 3-5 cells wide, but sometimes only 1 or 2, and occasionally up to 15, cells wide; high to very high; markedly heterogeneous, sometimes composed entirely of square and upright cells. **Fibres** typically septate; pits simple to distinctly bordered, limited to the radial walls; of medium length to very long.

LEAF

Generally dorsiventral but sometimes centric; consisting entirely of palisade tissue in *Xylosma ellipticum* Tul. **Hairs** of several types. (i) Simple, uni-

cellular in *Carrierea* and *Itoa*; unicellular with blunt protuberances in *Hopelstigma*. (ii) Simple, unicellular, sclerenchymatous trichomes in *Banara*, *Byrsanthus*, *Calantica*, *Casearia*, *Homalium*, *Samyda*, *Tetrathylacium*, *Zuelania*. (iii) Tufted hairs in certain species of *Banara*, *Casearia*, *Ryania*. (iv) Two-armed hairs in *Banara* sp. and *Homalium* sp. (v) Stellate hairs recorded in species of *Banara*, *Homalium*, *Kiggelaria*, *Patrisia*, *Pineda*. (vi) Peltate hairs in *Mayna* and probably other members of the Oncobeeae. (vii) Uniseriate hairs with thin walls between the component cells in *Casearia*, *Samyda*, *Zuelania*. (viii) Uniseriate, glandular hairs, sometimes very long and provided with a rounded terminal cell, in *Hopelstigma*. Wart-like **emergences**, stated to function as hydathodes, recorded on the petiole at the ends of vascular bundles in *Scolopia*. **Epidermis** characterized by the presence of crystal-idioblasts in species of *Bembicia*, *Camptostylus*, *Casearia* (many spp. idioblasts sometimes very large), *Dasylepis*, *Erythrospermum*, *Itoa*, *Laetia*, *Ludia*, *Lunania* (many spp.), *Oncoba*, *Ophiobotrys*, *Osmelia*, *Poggea*, *Pyramido-carpus*, *Rawsonia*, *Samyda*, *Scolopia*, *Xylosma*, *Zuelania* (in some members of the Apocynaceae similar crystals occur in the epidermis). Pits in the walls of the epidermal cells not uncommon, and also secondary tangential divisions of the cells in *Scolopia* and probably other genera. Epidermis composed of mucilaginous cells in species of *Gerrardina*, *Paropsia*, and *Neumannia*; papillose in *Idesia* sp. and on the lower surface in *Berberidopsis*. Inner and lateral walls of the epidermal cells thickened in *Laetia coriacea* Spruce. **Cuticle** exhibiting markings comparable with those on etched glass recorded in *Aphaerema*, *Banara*, *Bembicia*, *Byrsanthus*, *Calantica*, *Casearia*, *Dissomeria*, *Euceraea*, *Gerrardina*, *Homalium*, *Lunania*, *Ophiobotrys*, *Osmelia*, *Pyramido-carpus*, *Samyda*, *Tetrathylacium*, *Zuelania*. Wedge-shaped ridges of cuticle, stated to be very striking in surface view, recorded in *Banara brasiliensis* (Gray) Benth. **Wax** present on the surface in certain species of *Laetia* and *Oncoba*. **Hypoderm** of one to several layers present beneath the upper epidermis in species of *Banara*, *Byrsanthus*, *Casearia* (many spp.), *Dasylepis*, *Erythrospermum*, *Euceraea*, *Homalium*, *Itoa*, *Kiggelaria*, *Laetia*, *Ludia*, *Xylosma*, and *Zuelania*. **Stomata** generally confined to the lower surface, but recorded on the upper surface as well in *Casearia* and *Lunania*; rubiaceous in species of *Banara*, *Bembicia*, *Berberidopsis*, *Byrsanthus*, *Calantica*, *Carrierea*, *Casearia*, *Dissomeria*, *Euceraea*, *Flacourtia*, *Homalium*, *Itoa*, *Laetia*, *Ludia*, *Mayna*, *Oncoba*, *Pangium*, *Samyda*, *Xylosma*, *Zuelania*; cruciferous in species of *Centroplacus*, *Neumannia*, *Osmelia*, and *Rawsonia*; with a tendency towards the cruciferous type in *Erythrospermum*, *Hydnocarpus*, *Kiggelaria*, *Mayna*. Stomata appearing as islands owing to the contrast between the thin-walled subsidiary cells and the surrounding thick-walled pitted cells of the remainder of the epidermis on the lower surface of *Banara portoricensis* Urb. **Mesophyll** containing sclerenchymatous fibres in certain species of *Calantica*, *Casearia*, *Homalium*, *Zuelania*. Simple and branched sclerenchymatous idioblasts (spicular cells) recorded in species of *Centroplacus*, *Erythrospermum*, *Patrisia*, and *Ryania*. Arm-palisade cells recorded in *Casearia*. Upper layers of the spongy mesophyll strongly thickened and filled with brown contents in many species of *Lunania*. Vascular bundles of the smaller **veins** generally accompanied on both the upper and lower sides, or wholly surrounded by a thick ring of sclerenchyma. Vascular bundles in the larger veins of *Erythrospermum*

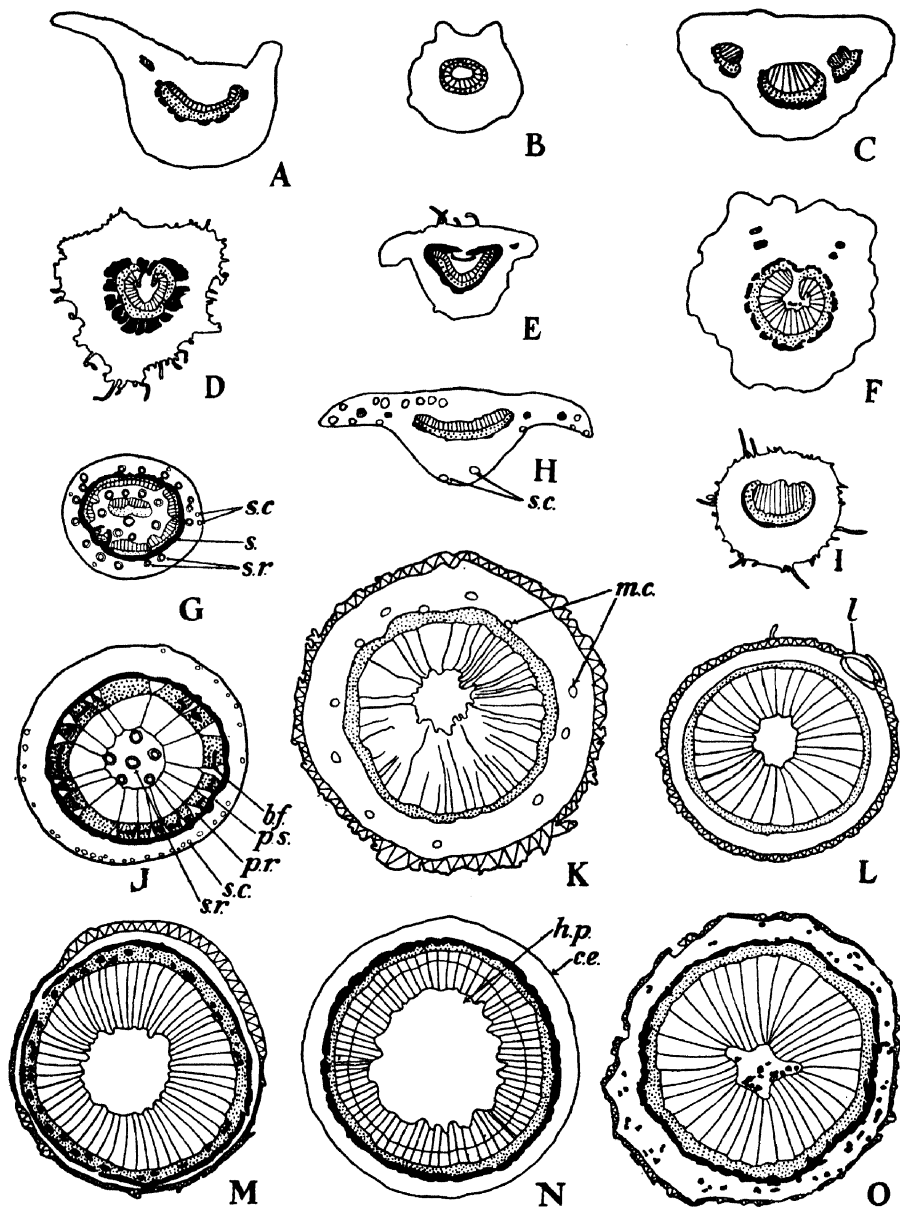


FIG. 30. *FLACOURTIACEAE*, A-C, E-F, I, L-O; *BIXACEAE*, G and J; *CANELLACEAE*, H and K; *THYMELAEACEAE*, D

A, *Dovyalis caffra* (Hook. f. et Harv.) Warb. Petiole $\times 15$; sclerosed cells on the adaxial side of the vascular arc not shown. B, *Oncoba spinosa* Forsk. Petiole $\times 15$. C, *Azara gilliesii* Hook. et Arn. Petiole $\times 15$. D, *Solmsia calophylla* Baill. Petiole $\times 15$. E, *Gerrardina foliosa* Oliver. Petiole $\times 15$. F, *Homalium africanum* Benth. Petiole $\times 9$. G, *Bixa orellana* Linn. Petiole $\times 10$. H, *Canella alba* Murr. Petiole $\times 15$. I, *Azara dentata* Ruiz. et Pav. Petiole $\times 15$. J, *Bixa orellana* Linn. Young stem $\times 10$. K, *Canella alba* Murr. Stem $\times 15$. L, *Azara dentata* Ruiz. et Pav. Stem $\times 15$. M, *Homalium africanum* Benth. Stem $\times 9$. N, *Berberidopsis corallina* Hook. f. Stem $\times 15$. O, *Asteropeia sphaerocarpa* Baker. Stem $\times 7$.

b.f. Phloem fibres. c.e. Cutinized epidermis. h.p. Hollow pith. l. Lenticel. m.c. Mucilage canal. p.r. Primary rays broadening in the phloem. p.s. Pericyclic sclerenchyma. s.c. Secretory cells. s.r. Secretory canal.

sp. forming an almost closed ring. Midrib of *Dipentodon sinicus* Dunn. with crescent-shaped groups of xylem and phloem, with additional phloem groups on the adaxial side between the ends of the crescent, the whole strand being surrounded by a broad cylinder of fibres. **Petiole**, in transverse sections through the distal end of material examined at Kew, exhibiting the following types of structure. (1) Median petiolar vascular strand solitary and crescentic. (a) Vascular strand shallow, with sclerosed cells between the ends of the vascular crescent in *Dovyalis caffra* (Hook. f. et Harv.) Warb. (Fig. 30 A). (b) Vascular strands thick, slightly crescentic, sometimes with sclerosed cells between the ends of the crescent in *Azara dentata* Ruiz. et Pav. (Fig. 30 I), and *Flacourtia prunifolia* H.B. et K. Structure somewhat similar in *Homalium africanum* Benth. (Fig. 30 F). (c) Vascular strand of *Gerrardina foliosa* Oliv. deeply crescentic and strongly supported by thick-walled fibres in the pericyclic region, inwardly directed strands of fibres extending towards each other from the ends of the vascular crescent without quite meeting. (d) Vascular strand crescentic with strongly incurved ends in *Berberidopsis corallina* Hook. f. An arc-shaped vascular strand, accompanied by smaller ones towards the wings, also noted in *Carrierea calycina* Franch. (2) Vascular arc dissected. (a) Median vascular strands of *Kiggelaria africana* Linn. slightly interrupted and provided with inwardly directed ends, the xylem including well-marked radial multiples of thick-walled vessels. (b) Vascular system of *Azara gilliesii* Hook. et Arn. (Fig. 30 C) dissected into several distinct strands (3) Median vascular strand cylindrical. (a) Vascular strand circular in *Hydnocarpus wightiana* Blume and *Oncoba spinosa* Forsk. (Fig. 30 B), the xylem including very well-marked, radial multiples of thick-walled vessels. (b) Vascular strand cylindrical, but adaxially flattened or slightly concave in *Poliothyrsis sinensis* Oliv., the thick-walled xylem vessels being in well-marked radial multiples.

Cluster **crystals** very common and often abundant; observed in the cortical region of the petiole in species of *Azara*, *Berberidopsis*, *Dipentodon*, *Dovyalis*, *Flacourtia*, *Gerrardina*, *Homalium*, *Hydnocarpus*, *Kiggelaria*, *Oncoba*, *Poliothyrsis*, *Rawsonia*. Bodies resembling **cystoliths** recorded in *Homalium*. (See also under 'Epidermis'.) **Secretory cavities** (described as resin glands by Gilg, 773) not always conspicuous in dried material, present in the mesophyll of most species of *Casearia*, and commonly or occasionally also in *Laetia*, *Lunania*, *Osmelia*, *Samyda*, *Zuelania*.

AXIS

YOUNG STEM (Fig. 30 L-O)

Structure rather imperfectly known. **Cork** superficial in origin in most of the species investigated; consisting of thin-walled cells in species of *Azara*, *Dovyalis*, *Hydnocarpus*, *Poliothyrsis*. **Pericycle** including isolated strands of fibres, sometimes united to form a composite ring. Isolated strands of fibres recorded in species of *Azara*, *Dasylepis*, *Dendrostylis*, *Grandidiera*, *Gynocardia*, *Oncoba*. A composite and continuous ring of sclerenchyma present in species of *Banara*, *Casearia*, *Dipentodon*, *Homalium*, *Hydnocarpus*, *Poliothyrsis*, *Ryana*, *Taraktogenos*; a sclerenchymatous ring composed of slightly elongated parenchymatous cells recorded in a species of *Physena*. **Phloem** of *Erythrospermum*, like that of the Bixaceae and Cochlospermaceae, traversed by enlarged distal ends of the medullary rays, the rays appearing

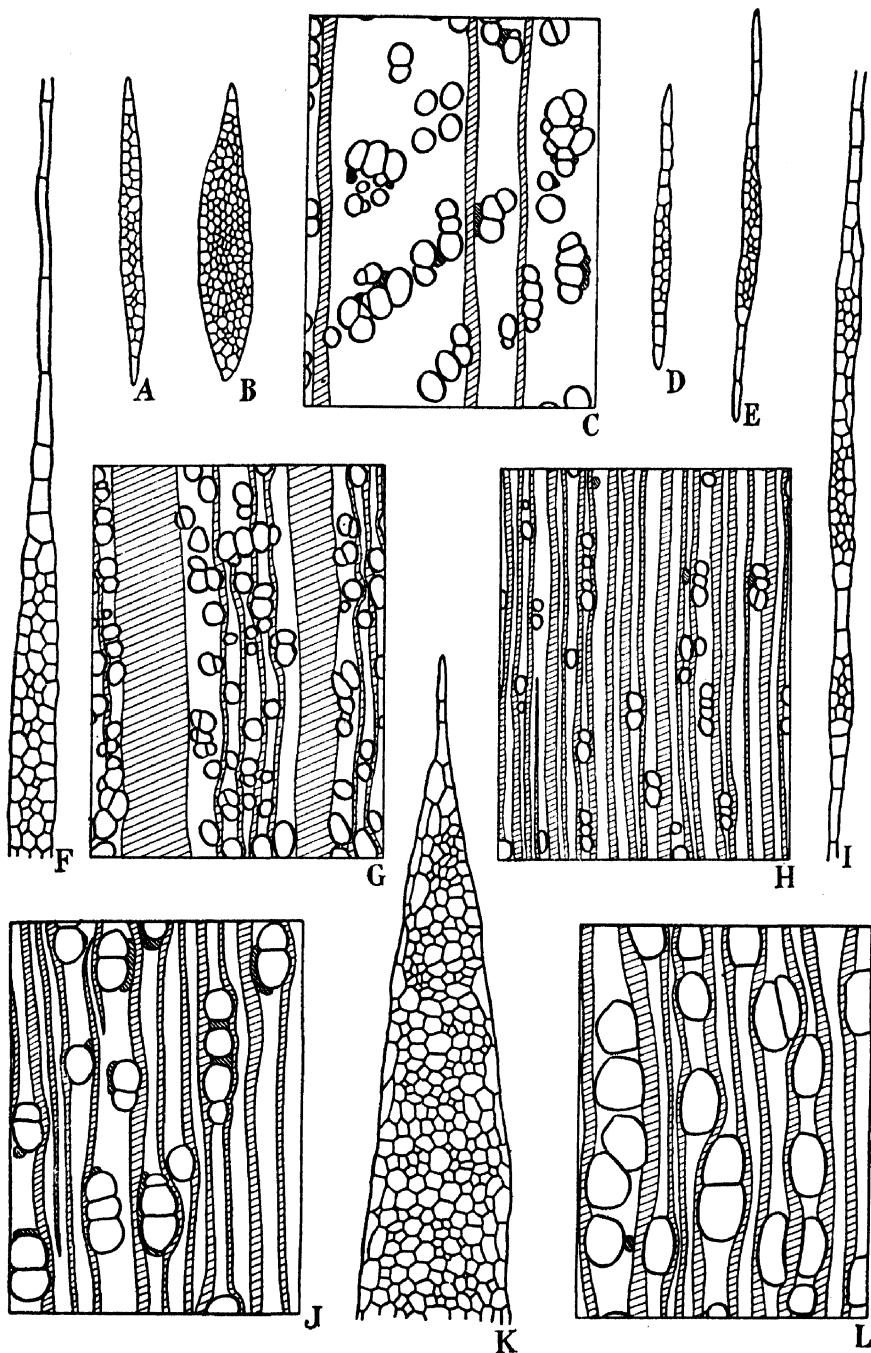


FIG. 31. *PITOSPORA*CEAE, A-C; *FLACOURTIA*CEAE, D-L

A, *Pittosporum ferrugineum* (Dryand.) Ait. B, *Bursaria spinosa* Cav. C, *Pittosporum ferrugineum* (Dryand.) Ait. D, *Idesia polycarpa* Maxim. E, *Homalium tomentosum* Benth. F, *Casearia gladiiformis* Mast. G, *Ryania speciosa* Vahl. H, *Dovyalis zxyphoides* E. Mey. I, *Homalium longifolium* Benth. J, *H. smythesi* Hutch. et Dalz. K, *Ryania speciosa* Vahl. L, *Taraktogenos kunstleri* King.

triangular in transverse sections. Rays in other investigated members of the Flacourtiaceae not enlarged in the phloem. **Phloem** and **xylem**, in most of the genera examined, forming continuous cylinders traversed only by narrow rays. Thick, longitudinal strands of stone cells present in the phloem of *Homalium africanum* Benth. Vessels mostly with simple perforations but occasionally with scalariform plates, the latter occurring especially in the primary wood, e.g. in *Homalium africanum* (see also 'Wood'). **Pith** very heterogeneous in *Berberidopsis corallina* Hook. f.

Crystals frequently very abundant, their nature and distribution often characteristic of and helpful in identifying genera and species.

The following more detailed observations were made on material grown at Kew.

(i) Solitary crystals in the inner part of the primary cortex of *Casearia* sp., *Dovyalis caffra* (Hook. f. et Harv.) Warb., *Flacourtia prunifolia* H.B. et K., *Homalium africanum* Benth., *Hydnocarpus wightiana* Blume, *Oncoba spinosa* Forsk.

(ii) Solitary crystals in some of the stone cells of the pericycle in *Casearia* sp., *Dovyalis caffra*, *Flacourtia prunifolia*, *Homalium africanum*, *Hydnocarpus wightiana*, *Oncoba spinosa*, *Poliothyrsis sinensis* Oliv.

(iii) Solitary crystals abundant in the soft tissues of the phloem of *Homalium africanum* and *Oncoba spinosa*.

(iv) Large solitary crystals in the pith of *Azara dentata* Ruiz. et Pav., *Azara gilliesii* Hook. et Arn., *Dovyalis caffra*, *Flacourtia prunifolia*, *Hydnocarpus wightiana*, *Oncoba spinosa*, *Poliothyrsis sinensis*, *Rawsonia lucida* Harv. et Sond.

(v) Cluster crystals abundant in the cortex of *Berberidopsis corallina* Hook. f. and *Kiggelaria africana* Linn.

(vi) Cluster crystals infrequent in the cortex of *Dipentodon sinicus* Dunn., *Dovyalis caffra*, *Homalium africanum* Benth., *Poliothyrsis sinensis*, *Rawsonia lucida*.

(vii) Cluster crystals abundant in the phloem in *Azara dentata*, *Azara gilliesii*, *Casearia* sp., *Dovyalis caffra*, *Homalium africanum*, *Hydnocarpus wightiana* (not very numerous), *Kiggelaria africana*.

(viii) Cluster crystals in the pith of *Azara gilliesii*, *Hydnocarpus wightiana*, *Kiggelaria africana*, *Poliothyrsis sinensis* (only in very young stems), *Rawsonia lucida*.

(ix) Crystals of all kinds relatively scarce in *Gerrardina* spp.

The above information concerning crystals could usefully be elaborated by further investigation.

Secretory cells, whose contents are stained deeply with haematoxylin, abundant in the parenchymatous tissues of *Berberidopsis corallina* and *Rawsonia lucida*.

WOOD (Fig. 31 D-L)

Vessels usually moderately small (50–100 μ mean tangential diameter), sometimes slightly larger, e.g. in some species of *Ahernia*, *Mesaulospermum*, *Pangium*, *Peridiscus*, *Tetrathylacium*, and *Trichadenia*, or smaller, e.g. in some species of *Carpotroche*, *Dovyalis*, *Rawsonia*, *Trimeria*, and *Xylosma*. Solitary

and in radial multiples of 2 or 3 cells; multiples of 4 or more cells sometimes moderately common locally or in particular species, e.g. of *Flacourtia*, *Hydnocarpus*, *Kiggelaria*, *Trimeria*, and *Xylosma*; individual vessels or groups often separated radially by only a single flattened fibre; sometimes in small clusters. Usually 10–50 per sq. mm., but sometimes fewer (5–9) in species of *Pangium*, *Ryparosa*, and *Trichadenia* and more numerous (50–110) in species of *Azara*, *Gossypiospermum*, *Ludia*, *Prockia*, *Rawsonia*, *Ryania*, *Samyda*, *Trimeria*, and *Xylosma*. Spiral thickening reported in *Azara*, *Hisingera*, *Olmediella*, *Poliothyrsis*, and *Xymalos* (1851). Perforation plates simple and oblique in most genera, but with some scalariform plates in addition (usually with few bars and sometimes rare), in *Aberia* (2158), *Ahernia*, *Azara*, *Caloncoba*, *Casearia* p.p., *Dendrostylis* (2158), *Dovyalis*, *Gynocardia*, *Hasseltia*, *Homalium*, *Lunania*, *Olmediella*, *Oncoba*, and *Ryparosa*; with occasional scalariform plates in the neighbourhood of the primary wood in *Banara* (2430), *Carpotroche*, *Casearia* (2430), *Grandidiera* (2158), *Idesia*, *Lindackeria*, *Mayna*, and *Trimeria* (2158); all or predominantly scalariform in *Asteriostigma*, *Azara* p.p. (2158), *Bergsmia* (1154), *Carpotroche* p.p. (2430), *Dasylepis*, *Erythrospermum*, *Hasseltiopsis* (1886), *Hydnocarpus*, *Peridiscus*, *Rawsonia*, *Scottellia*, *Taraktogenos*, and *Tetrathylacium*. Janssonius (1154) refers to scalariform plates in *Pangium edule* Reinw. Sometimes with a few reticulate or foraminate plates, e.g. in *Hydnocarpus* and *Rawsonia*, and occasionally with scalariform or reticulate plates to ray cells, even in woods in which the normal perforations between members are simple, e.g. in *Trichadenia*. Intervascular pitting scalariform in *Hasseltia* and opposite or transitional in *Erythrospermum*, *Hydnocarpus*, *Mayna*, *Peridiscus*, and *Ryparosa* p.p., alternate in the others; the alternate pitting very small to minute, and the pits to ray cells similar [though sometimes with several pits subtended by one ray pit (unilaterally compound), e.g. in *Ryania*] in *Banara*, *Casearia*, *Flacourtia*, *Gossypiospermum*, *Hecatospermum*, *Homalium*, *Laetia* (1886), *Ludia*, *Lunania*, *Ophiobotrys*, *Osmeia*, *Prockia*, *Ryania*, *Samyda*, *Scolopia*, *Trichadenia*, *Trimeria*, *Xylosma*, and *Zuelania*; pits large in the other genera with alternate pitting and the pitting to rays in these and the genera with scalariform and opposite intervacular pitting commonly elongated and often scalariform, e.g. in *Ancistrothyrsus* (1886), *Arechavaletaia* (1886), *Asteriastigma*, *Azara*, *Dasylepis*, *Carpotroche*, *Dovyalis*, *Erythrospermum*, *Hasseltia*, *Hasseltiopsis* (1886), *Kiggelaria*, *Lindackeria*, *Olmediella*, *Pangium*, *Peridiscus*, *Rawsonia*, *Ryparosa*, *Scottellia*, *Tetrathylacium*, *Trichadenia*, and *Taraktogenos*. Tyloses occasionally present and, according to Record and Hess (1886), fairly abundant in *Ancistrothyrsus* (sometimes sclerotic), *Lindackeria*, and *Peridiscus*. Gonggrijp (794) refers to silica in the tyloses of *Hydnocarpus* and *Taraktogenos*. Mean member length most commonly 0.7–1.3 mm. and up to 1.7 mm. in *Taraktogenos*. **Parenchyma** absent or very sparse. When present, paratracheal and usually limited to isolated cells touching the vessels (Fig. 31 J), but Record and Hess (1886) describe the parenchyma as ‘irregularly paratracheal, short aliform and diffuse’ in *Ancistrothyrsus* and as ‘reticulate’ in *Peridiscus*; Williams (2430) refers to fine lines in *Lindackeria* and *Lunania*, but these were not present in the material available to the author. Moderately abundant about the vessels and scattered among the fibres in *Pangium edule* Reinw. In *Aphloia* what appear in transverse sections to be diffuse parenchyma cells are thin-walled

septate fibres (see below). Record and Hess (1886) note chambered crystals in *Olmediella*. **Rays** most commonly up to 3–5 cells wide, but up to 6–8 cells in some species of *Banara*, *Rawsonia*, and *Scottellia* and 10 or more cells wide in *Aphloia*, *Patrisia* (2430), and *Ryania*; seldom more than 2 cells wide in some species of *Casearia*, *Idesia*, and *Xylosma* and almost exclusively uniseriate in *Asteriastigma macrocarpa* Bedd. Typically high and often over 3 mm. high, but seldom more than 1 mm. high in *Dovyalis*, *Idesia*, and some species of *Homalium*. Uniseriates numerous and composed of high upright cells. Rays 8–24, mostly 9–15 per mm. Markedly heterogeneous (Kribs's Type I), typically with 10 or more marginal rows of square or upright cells, but sometimes with only 4–10 rows, e.g. in *Homalium tomentosum* Benth., *Idesia polycarpa* Maxim., *Pangium edule* Reinw., and *Scottellia coriacea* A. Chev. The multiseriate rays sometimes composed entirely of square and upright cells, e.g. in *Casearia nitida* (L.) Jacq. and *Lindackeria dentata* Gilg, as also are the wholly uniseriate rays of *Asteriastigma macrocarpa*. Occasionally with sheath cells (1154). Vertically fused rays common (Fig. 311). Nearly always containing crystals, which are often abundant; sometimes apparently chambered¹ or chambered when occurring in the upright cells, e.g. in *Banara*, *Flacourtia*, *Homalium*, *Prockia*, *Scolopia*, *Trimeria*, and *Xylosma*. 'Perforated ray cells' reported in several genera (358). **Fibres** septate, except in *Ancistrothyrsus* and *Peridiscus* (1886) and septa rare or absent from *Ludia*. Pits almost entirely limited to the radial walls, simple or with small, and often very indistinct, borders, but with large, distinct borders in *Aphloia* and in *Ancistrothyrsus* and *Peridiscus* (1886). In *Aphloia* the ground tissue consists of thick-walled fibres with conspicuous bordered pits, among which are scattered thin-walled septate fibres, which are distributed as single cells or short uniseriate lines resembling diffuse parenchyma; the thick-walled fibres also are septate in *A. myrtiflora* Galpin, but not in *A. mauritiana* Baker; the parenchyma-like septate fibres have bordered pits and in both these and the thick-walled fibres the pits are equally numerous in both radial and tangential walls. Walls moderately thin to very thick in the other genera and often with a gelatinous layer. Mean length 0.9–2.7, most commonly about 1.6 mm., and 2.0 mm. or more in *Homalium*, *Pangium*, *Taraktogenos*, and *Xymalos*.

DIONCOPHYLLUM PELTATUM Hutch. et Dalz.

An anomalous liane with successive bundles of xylem and phloem, without regular arrangement.

Vessels very large, mostly solitary, but with some pairs and multiples; about 2 per mm. Perforations simple. Intervascular pitting alternate and large, often with coalescent apertures; pits to parenchyma similar. **Parenchyma** (a) conjunctive, between the bundles; containing scattered, large, solitary, and often spindle-shaped stone cells; (b) paratracheal, as narrow sheaths round the vessels (vasicentric); and (c) apotracheal, as a few cells

¹ Record and Hess (1886) draw attention to the fact that these cells are not, strictly speaking, 'chambered' in the sense that each crystal is enclosed in a separate cell and not merely separated from the next by a septum. The genuinely chambered groups of crystals that occur in *Banara* are described by these authors as occurring in the fibres; in the material examined of *Banara guianensis* Aubl. such crystals were observed only in the very tall upright cells of the rays.

scattered among the fibres. **Rays** uniseriate; short to moderately high; continuing through the individual bundles, but varying in direction from bundle to bundle. **Fibres** with large, conspicuously bordered pits that are equally numerous on both radial and tangential walls, the borders smaller than those of the intervacular pitting. Walls moderately thick.

BARK

According to Sprague and Boodle (2173) the bark of *Casearia praecox* Griseb. exhibits the following characters. Cork cells thickened on the inner side, their cavities becoming nearly or quite obliterated. Secondary phloem containing secretory canals and stone cells, the former provided with a thin-walled epithelium, the contents being soluble in alcohol. The stone cells in the older part of the secondary phloem form continuous or nearly continuous zones alternating with soft tissue, but in the younger phloem are arranged in rounded groups or tangential bands. Solitary crystals of calcium oxalate present in the stone cells.

ANOMALOUS GENERA

The following genera are treated separately since their taxonomic positions are uncertain, whilst the facts recorded about their anatomical structure do not appear to conform, at least in certain respects, with those of the Flacourtiaceae.

(i) ASTEROPEIA

LEAF

Dorsiventral. **Hairs** not observed. **Epidermis** strongly cutinized. **Stomata** confined to the lower surface, each surrounded by about 12 cells similar to those of the remainder of the epidermis; guard cells very strongly cutinized. Aqueous **hypoderm**, about 2 or 3 cells wide, situated below the upper epidermis in *A. sphaerocarpa* Baker, but 4 or 5 layers recorded by Beauvisage (163) in other species. **Mesophyll** consisting of 3 or 4 layers of palisade cells (with corrugated anticlinal walls in herbarium material) and an extensive spongy region, the latter containing rounded sclerenchymatous idioblasts with short arms. Similar idioblasts also present in the collenchyma above the median vein. Vascular bundles of the **veins** embedded in the mesophyll and supported by sclerenchymatous sheaths. **Petiole**, in transverse sections through the distal end, exhibiting an almost closed but dorsally flattened vascular strand in which the phloem is as broad as or locally even broader than the xylem, the whole vascular system being surrounded by an almost continuous ring of sclerenchyma, and enclosing a few sclerosed elements in the medullary region.

AXIS

YOUNG STEM

Cuticle very thick. **Cork** arising in the sub-epidermis. **Cortex** containing rounded or angular sclerenchymatous idioblasts sometimes with short arms, either isolated or arranged in groups. **Pericycle** demarcated externally by a composite, continuous ring of sclerenchyma and including a few stone cells in the inner part. **Phloem** and **xylem** in the form of continuous cylinders,

traversed by uniseriate rays. Phloem apparently containing secretory cavities, but their true nature could not be determined in the herbarium material examined. Vessels mostly solitary, rather unevenly distributed, usually circular or slightly oval in transverse section, seldom exceeding $50\ \mu$ in radial diameter; perforations simple. **Pith** somewhat heterogeneous, including solitary and grouped sclerosed cells.

With regard to the secondary xylem of *Asteropeia*, the only material available was a single specimen of *A. rhopaloides* Bak., which had not been correlated with herbarium material. It differed markedly from the rest of the family, e.g. in having minute, alternate intervacular pitting and pits to ray cells, solitary vessels and exclusively uniseriate rays.

SPECIES OF *ASTEROPEIA* DESCRIBED

The above description is based on an examination of *Asteropeia sphaerocarpa* Baker in the Kew Herbarium. It differs only in minor respects from other species such as *A. multiflora* Dup-Th. and *A. ambylocarpa* Tul. previously described by Beauvisage (163).

(ii) PSILOXYLON

Secretory cavities recorded in the mesophyll as well as in the cortex of young stem. **Cork** arising in the pericycle, and consisting of layers composed respectively of flattened, thin-walled cells and thickened cells with relatively wide lumina. **Pericycle** demarcated by sclerenchyma consisting wholly of stone cells. Secondary **phloem** devoid of fibres, but including layers of cells filled with cluster crystals. **Intraxylary phloem** recorded.

Solereder considered that this genus should be placed in the Myrtaceae.

(iii) FROPIERA

The anatomy of this genus needs further investigation. The leaves probably contain **secretory cavities**.

(iv) HASSELTIA AND PROCKIA

Phloem containing secretory cells with yellow contents resembling gum-resin, and which are more abundant in *Hasseltia* than *Prockia*. Sclerenchymatous elements said to be absent from the pericycle and phloem.

(v) PLAGIOPTERON

Secretory elements resembling **latex canals** are present in the phloem in the veins of the leaf as well as in the phloem and pith of the axis. These elements contain a rubber-like substance which can be drawn out in the form of fine threads when the leaf is broken.

TAXONOMIC NOTES

Most of the genera which were included by Bentham and Hooker in the Bixaceae and Samydaceae are characterized by stomata of the rubiaceous or cruciferous types and the presence of crystal idioblasts in the epidermis of the leaf. These characters together suggest that these genera should be combined into a single family, which in practice conforms approximately with the Flacourtiaceae as understood by Gilg (768). This is also in agreement with

the views of modern taxonomists who base their conclusions on external morphological characters. The group thus constituted is also very homogeneous as regards its wood anatomy, though the genera differ considerably in the degree of specialization of the vessels. Record and Hess (1886), however, note that 2 genera, *Ancistrothyrsus* and *Peridiscus*, seem to be rather out of place. Only one line of subdivision suggests itself, the distinction between the genera with minute intervacular and vessel-ray pitting and the others. In the present account, however, the Flacourtiaceae-Paropsieae and Abatieae in the sense used by Gilg (768) have been described under Passifloraceae. *Bixa* has been regarded as the sole representative of the Bixaceae, whilst *Amoreuxia*, *Cochlospermum*, and *Sphaerosepalum* have been described under Cochlospermaceae. It will be seen that these last 4 genera differ from the Flacourtiaceae, but are, with the possible exception of *Sphaerosepalum*, very different from one another. It seems to be largely a matter of opinion whether the Bixaceae and Cochlospermaceae should be recognized as distinct or united into one family. On anatomical grounds they are not very clearly demarcated, except in so far as the woods of *Bixa* and *Cochlospermum* are clearly distinguishable by their parenchyma. (See also under 'Bixaceae' and 'Cochlospermaceae'.) The genus *Erythrospermum* which tends to conform with the Tiliaceae in the possession of rays which broaden out in the phloem, on external morphological characters and in its wood anatomy, agrees rather with the Flacourtiaceae. *Dipentodon* has been included in the Flacourtiaceae rather than in the Celastraceae on the advice of Dr. T. A. Sprague, especially as the anatomical structure conforms with this suggestion. The family also includes several genera whose true taxonomic position has not yet been finally established. These have been described separately, partly to emphasize the points in which they differ from most members of the family, and partly to facilitate their transfer to other families if this should become necessary in the future. The genera concerned are *Asteropeia*, *Fropiera*, *Hasseltia*, *Plagiopteron*, *Prockia*, and *Psiloxylon*. The Flacourtiaceae are distinguished from the Bixaceae and Tiliaceae by the lack of mucilage receptacles in the cortex and pith of the young stem, and from the Violaceae by the possession of crystal-idioblasts in the epidermis.

The following views, based on a study of wood structure, have also been expressed by Vestal (2239). He regards the Cistaceae as derived from the Bixaceae and these in turn 'stem' from the Flacourtiaceae, with the Cochlospermaceae as a parallel development also arising in the Flacourtiaceae. Of these families he says 'the Flacourtiaceae are the only ones that show in their anatomy any relationship to the Dilleniaceae'.

Vestal opposes Hutchinson's view that this group is basic for the Theales and Guttiferales, on the grounds that it is 'rather difficult to conceive of the obviously primitive vessel members in the Theaceae, Actinidiaceae and Saurauaceae as coming from the highly evolved vessel members of the Bixales series'. It is, however, open to question whether the vessels of the Flacourtiaceae can be correctly described as 'highly evolved' in view of the occurrence of scalariform intervacular pitting, entirely scalariform perforation plates and mean member lengths of over 2 mm. in several genera. (Cf. Actinidiaceae 0.7 mm., Saurauaceae 1.5 mm., and Theaceae mostly 1.0-1.6 and 2.4 in *Adinandra*.)

ECONOMIC USES

Kei Apples are the fruits of *Dovyalis caffra* (Hook. f. et Harv.) Warb. The fruits of certain *Flacourtia* spp. and *Oncoba spinosa* Forsk. are edible. Chaulmoogra Oil is obtained from the seeds of *Taraktogenos kurzii* King, whilst a similar oil is obtained from *Hydnocarpus* spp. West Indian Boxwood is derived from *Casearia praecox* Griseb.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aphaerema, Asteropeia,* Azara,* Banara, Bembicia, Berberidopsis,* Byrsanthus, Calantica, Camptostylus, Carrierea,* Casearia,* Centroplacus, Dasylepis, Dipentodon,* Dissomeria, Dovyalis,* Erythrospermum, Eucraea, Flacourtia,* Fropiera, Gerrardina,* Grandidiera, Gynocardia, Hasseltia, Homalium,* Hopelstigma, Hydnocarpus,* Idesia, Itoa, Kiggelaria,* Laetia, Ludia, Lunania, Mayna, Neumannia, Oncoba,* Ophiobotrys, Osmelia, Pangium, Patrisia, Physena, Pineda, Plagiopteron, Poggea, Poliothyrsis,* Prockia, Psiloxylon, Pyramidocarpus, Rawsonia,* Rynia (or *Patrisia*), Samyda, Scolopia, Taraktogenos, Tetrathylacium, Tisonia, Trimeria, Xylosma, Zuelania.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(‘Abatia’), (Aberia, or *Dovyalis*), Ahernia, (Ancistrothyrsus), Aphloia (or *Neumannia*), (Arechavaletaia), Asteriastigma, Asteropeia, Azara, Banara, (Bennettia), (Bergsmia, or *Ryparosa*), Caloncoba, Carpotroche, Casearia, Dasylepis, (Dendrostylis, or *Mayna*), Dioncophyllum, Dovyalis, Eleutherandra, Erythrospermum, (Grandidiera), Gossypiospermum, Gynocardia, Hasseltia, (Hasseltiopsis), Hecatostemon, (Hisingera, or *Xylosma*), Homalium, Hydnocarpus, Idesia, Kiggelaria, Laetia, Lindackeria, Lunania, Mayna, Olmediella, Oncoba, Ophiobotrys, Osmelia, Pangium, (Patrisia), Peridiscus, (Poliothyrsis), Prockia, Rawsonia, Rynia (or *Patrisia*), Ryparosa, Samyda, Scolopia, Scottellia, Taraktogenos, Tetrathylacium, Trichadenia, Trimeria, Xylosma, Zuelania.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Braendlein 253, Gilg 768, 773, Harvey-Gibson and Horseman 916, Sprague and Boodle 2173.

(ii) *On Wood Structure*

Bannan 133, Benoist 170, den Berger 177, 179, 182, Besson 186, Burgerstein 310, Chalk and Chattaway 358, 362, Cooper 461, Coster 481, Desch 574, Giordano 786, Gonggrijp 794, Howard 1088, Janssonius 1154, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Pearson and Brown 1679, Record 1818, 1843, 1851, 1884, Record and Hess 1886, Stone 2206, Tang 2231, Tupper 2298, Vestal 2239, Williams 2430, Yamabayashi 2478.

35. PITTOSPORACEAE

(FIG. 31 on p. 120; FIG. 32 on p. 130)

SUMMARY

(i) GENERAL

A family of trees, shrubs, and climbers, occurring in the warmer regions of the Old World, and especially well developed in Australia. A constant and characteristic feature of the family is the presence of **secretory canals** in the pericycle of the stem, roots, and leaves. Similar canals occur also in the secondary phloem of older stems, but according to Solereder they are never present in the primary cortex or pith, although they have been found in the secondary cortex. The **stomata** are rubiaceous with 2 or more pairs of subsidiary cells parallel to the pore. There is usually little or no **sclerenchyma** in the family, mechanical support being provided by collenchymatous elements. The **hairs** may be: (i) Simple, uniseriate trichomes with 2 or 3 basal cells and a long terminal cell. (ii) Two-armed hairs with a short stalk. (iii) Club-shaped glandular hairs. Transitions between these types also occur. Calcium oxalate is generally present in the form of clustered and solitary **crystals**, whilst styloids occur in the phloem.

(ii) Wood

Vessels small; in numerous small multiples and clusters, often with a diagonal pattern; perforations simple; intervacular pitting alternate and small, pits to ray cells similar; members of medium length. **Parenchyma** sparse, vasicentric. **Rays** up to 3-7 cells wide, with few uniseriates and almost homogeneous. **Fibres** septate, of medium length to moderately short.

LEAF

Centric in a few species, but mostly dorsiventral. **Hairs**. (i) Uniseriate with 2 or 3 short basal cells and a long terminal cell in *Billardiera*, *Marianthus*, *Pronaya*, *Sollya*. (ii) Two-armed trichomes with a short stalk, the terminal cell sometimes being deciduous, in *Bursaria*, *Citriobatus*, *Pittosporum*. (iii) Club-shaped glandular hairs in *Hymenosporum* and certain species of *Bursaria* and *Pittosporum*. **Epidermis** with strongly thickened outer walls. Upper epidermis papillose in *Marianthus tenuis* Benth. Cells of the **epidermis** horizontally divided in certain species of *Pittosporum*; the inner layer elongated in a palisade-like manner in *P. phillyraeoides* DC. **Stomata** confined to the lower surface; rubiaceous, provided with 2 or several subsidiary cells parallel to the pore, the subsidiary cells generally having thinner walls than the remaining epidermal cells. **Petiole**, in transverse sections, e.g. of *Pittosporum tenuifolium* Gaertn. (Fig. 32 D), generally exhibiting an arc of 3, 5, 7 or more vascular strands, but a solitary vascular bundle recorded in certain species with small leaves; bundles not usually accompanied by sclerenchyma. **Crystals** of calcium oxalate clustered or solitary and sometimes present in specially large sacs. **Secretory canals** (see also under 'Axis') present.

AXIS

YOUNG STEM (Fig. 32 F)

Cork arising superficially in *Pittosporum* and *Sollya*; component cells with

thin to thick walls and filled with gum-like contents in the same 2 genera. Primary **cortex** generally collenchymatous especially in the outer portions. Secondary **phloem** also tending to become collenchymatous; sieve tubes with comparatively small lumina and scalariform sieve plates. **Xylem** in the form of a cylinder traversed by rather broad, lignified rays in *Pittosporum*, and by narrower rays in *Sollya heterophylla* Lindl. Vessels with simple perforations. **Pith** lignified. **Secretory canals** (see also 'Leaf'), with colourless, yellow or reddish contents, present especially in the inner part of the cortex and pericycle. Secretory canals stated to occur, although less frequently, in the phloem or pith of *Billardiera*, *Bursaria*, *Cheiranthera*, *Citriobatus*, *Hymenosporum*, *Marianthus*, *Pittosporum*, *Pronaya*, *Sollya*. **Crystals**, similar to those in the leaf, sometimes situated in large sacs, chiefly in the phloem. Styloids also recorded in the phloem.

WOOD (Fig. 31 A-C)

Vessels very to moderately small (mean tangential diameter 40–100 μ); solitary, in short radial multiples and in numerous clusters; sometimes with a distinct oblique or tangential pattern (Fig. 31 c); 25–50 per sq. mm. with spiral thickening in at least the tips of the members in some species of *Bursaria*, *Hymenosporum*, and *Pittosporum*; Solereder lists several other genera as having spiral thickening or spiral striations. Perforations simple, oblique. Intervascular pitting alternate, small to very small, pits to ray cells similar. Often containing a yellow substance in *Pittosporum*. Mean member length 0.45–0.9 mm. **Parenchyma** scanty, paratracheal, occurring as a few cells about the vessels. Very occasionally containing a few chambered crystals. Strands usually of 4 cells. **Rays** up to 3–7 cells wide; less than 1 mm. high; uniseriate rare, composed mainly of procumbent cells; 5–12 rays per mm.; almost homogeneous (Kribs's Types Het. II B to Hom. I), usually with a single marginal row of square cells (Fig. 31 B). Crystals present in the marginal cells, often in rounded, slightly larger cells in *Citriobatus* and *Pittosporum*. **Fibres** septate, but the septa sometimes rather few. Pits small and almost entirely limited to the radial walls, simple or with very small borders. Walls moderately thin. Mean length 0.8–1.1 mm.

ROOT

Secretory canals similar to those in the stem, present in the pericycle, situated externally to the xylem, as well as the phloem groups. Secretory canals stated to inhibit the development of lateral roots on the outer side of the xylem groups. Lateral roots in consequence arising between the secretory passage opposite a xylem group and the neighbouring secretory passage opposite a phloem group. Lateral roots stated to originate in a similar manner in the Araliaceae and Umbelliferae.

TAXONOMIC NOTES

Solereder (2158) and Guenet (832) have suggested on anatomical grounds that this family has affinities with the Umbelliferae and Araliaceae, an idea which was propounded by Van Tieghem and followed up by the authors just mentioned, but Pritzel (1758) thinks that the floral differences are too great to support this suggested relationship. Pritzel mentions that possible relationships

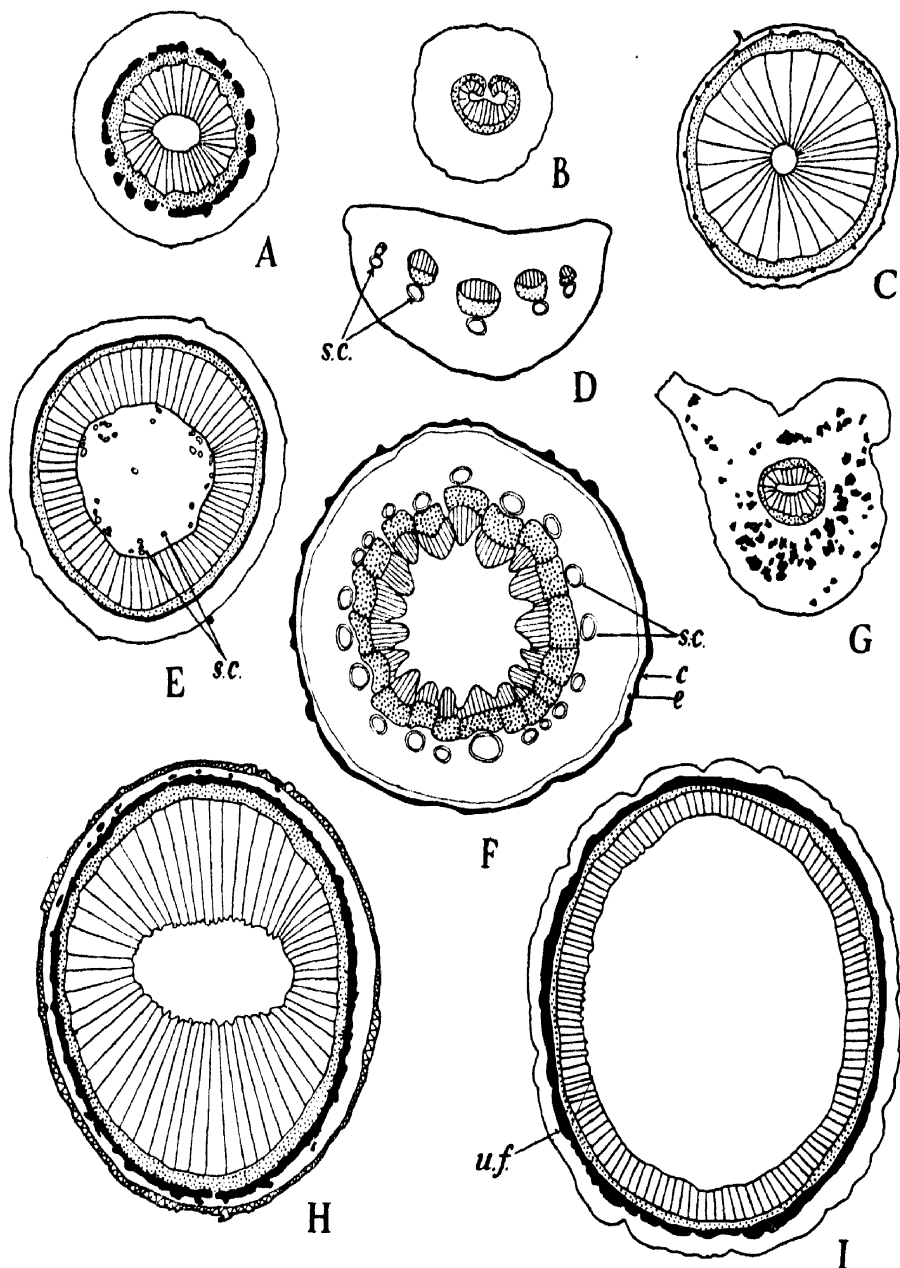


FIG. 32. *FRANKENIACEAE*, A; *POLYGALACEAE*, B and G-I; *TREMANDRACEAE*, C and E; *PITTOSPORACEAE*, D and F

A, *Frankenia laevis* Linn. Stem $\times 17$. B, *Barnhartia floribunda* Gleason. Petiole $\times 9$. C, *Platytheca galioides* Steetz. Stem $\times 17$. D, *Pittosporum tenuifolium* Gaertn. Petiole $\times 33$. E, *Tetradlea thymifolia* Sm. Stem $\times 17$. F, *Pittosporum tenuifolium* Gaertn. Young stem $\times 33$. G, *Moutabea guianensis* Aubl. Petiole $\times 9$. H, *Carpolobia alba* G. Don. Stem $\times 17$. I, *Polygala oppositifolia* Linn. Stem $\times 17$.

Fig. E. Abundant secretory cells with tanniniferous contents in all unlignified tissues.

c. Thick outer wall of epidermis. e. Epidermis. s.c. Secretory canals. u.f. Unlignified fibres.

between the Pittosporaceae on the one hand and such various families as Celastraceae, Escalloniaceae, Polygalaceae, Rhamnaceae, Tremandraceae, and Vochysiaceae on the other have been proposed from time to time. The septate fibres and paratracheal parenchyma of the Pittosporaceae suggest the Araliaceae as the nearest of the above families and make any relationship with the Escalloniaceae improbable. There are according to Pritzel difficulties about all of the possible relationships which have just been mentioned, so he prefers to regard the Pittosporaceae as a somewhat isolated family.

ECONOMIC USES

The woods of certain species of *Pittosporum* are of economic importance.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Billardiera, Bursaria, Cheiranthra, Citriobatus, Hymenosporum, Marianthus, Pittosporum,* Pronaya, Sollya.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Billardiera), Bursaria, (Cheiranthra), Citriobatus, Hymenosporum, (Marianthus), Pittosporum, (Pronaya), (Sollya).

LITERATURE

(i) *On General Anatomy*

Guenot 832, Pritzel 1758.

(ii) *On Wood Structure*

Baker 104, Brown, F. B. H. 280, Kanehira 1206, 1209, Record 1843, 1851, Yamabayashi 2478.

36. TREMANDRACEAE

(FIG. 32 on p. 130)

SUMMARY

This family of slender, heath-like shrublets, endemic in Australia, is fairly uniform in respect of its anatomical characters. The wood exhibits the following features. **Vessels** small, sometimes with spiral thickening, perforations simple. **Parenchyma** scanty paratracheal or absent. **Rays** 1-2 cells wide, composed of upright cells. **Fibres** with simple and bordered pits.

LEAF

Flat or linear, with margins frequently curved inwards towards the abaxial side. The shape of the leaf as seen in transverse section is stated to be of value for the identification of species. **Hairs**. (i) Simple, unicellular, stiff and thick-walled in *Tetratheca*. (ii) Stellate in *Tremandra*. (iii) Glandular, especially in *Tetratheca* and to some extent in *Platytheca*. **Mesophyll** including 1 layer of palisade cells. Inner walls of the cells of the **epidermis** frequently mucilaginous, except in *Tremandra*. **Stomata** confined to the lower surface; ranunculaceous. **Petiole**, in transverse sections, exhibiting a single vascular bundle, or 1 large and 2 small bundles. Calcium oxalate present in the form of solitary, and less frequently of clustered **crystals**.

AXIS

YOUNG STEM (Fig. 32 c and e)

Primary **cortex** of species of *Tetratheca* with reduced leaves containing palisade parenchyma. Bundles of sclerenchymatous fibres present in the 3 angles of species of *Tetratheca* with triangular branches. A composite, continuous ring of sclerenchyma recorded in the pericycle of *Tetratheca ciliata* Lindl. and *T. thymifolia* Sm.; strands of sclerenchyma observed in *Platytheca galioides* Steetz. **Xylem** in the form of a continuous cylinder traversed by narrow medullary rays. Stem almost wholly composed of secondary xylem in *Platytheca galioides* Steetz. (Fig. 32 c). Vessels in the same species small and angular; small but less angular in *Tetratheca thymifolia*. Perforations mostly simple, but occasional scalariform plates also recorded (see 'Wood'). **Pith** very narrow, consisting of cells with moderately thick, lignified walls in *Platytheca galioides*; much broader, somewhat heterogeneous and composed of a mixture of large empty thin-walled cells mixed with smaller ones filled with secreted material in *Tetratheca thymifolia*. **Secretory cells** with unidentified contents abundant in the unlignified tissues of *Tetratheca thymifolia*.

WOOD¹

Vessels very to extremely small; solitary and with a tendency to chains and multiples; with spiral thickening in *Platytheca galioides* Steetz. and *Tetratheca* spp. Perforations simple, but with a few scalariform plates near the primary wood in *Tremandra stelligera* R.Br. Intervascular pitting circular to oblong, usually in a single row owing to the small lumina of the vessels. Pits to ray and wood parenchyma often simple and oblong. **Parenchyma** scanty paratracheal or absent. Sometimes containing crystals. **Rays** 1-2 cells wide and composed almost entirely of upright cells; seldom more than 10 cells high. **Fibres** with small bordered pits in *Tetratheca glandulosa* Labill. and with both simple and bordered pits in the other genera. With fine spiral thickening in *Tetratheca efoliata* F. v. Muell.

TAXONOMIC NOTES

The affinities of this family have never been well established. Its anatomical features do not afford much assistance in arriving at a conclusion. In these circumstances the family must be regarded as somewhat isolated.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Platytheca,* Tetratheca,* Tremandra.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Platytheca), (Tetratheca), (Tremandra).

LITERATURE

On Wood Structure

Heimsch 938, Record 1800, 1851.

¹ Based almost entirely on the descriptions given by Solereder and by Heimsch (938).

37. POLYGALACEAE

(FIG. 32 on p. 130; FIG. 33 on p. 136; FIG. 91 on p. 402)

SUMMARY

(i) GENERAL

A family of herbs, shrubs, or rarely small trees occurring in both temperate and tropical regions. **Hairs** generally simple and unicellular, except in *Bredemeyera* and *Xanthophyllum* where they are sometimes uniseriate. The **stomata** are generally ranunculaceous, but sometimes tend to be rubiaceous. The midrib and **petiole** generally possess one vascular strand. Calcium oxalate occurs as solitary or clustered **crystals**. Lysigenous **secretory cavities** and **oil ducts** occur in *Polygala*. The **xylem** in transverse sections of young stems generally appears as a closed ring, even in herbaceous species, although according to Holm (1001, 1018), in certain North American species of *Polygala* there are about five collateral bundles in very young stems. For **Anomalous Structure** see under 'Wood'.

(ii) WOOD

Vessels small to large, usually exclusively solitary, perforations simple, intervacular pitting alternate, pits to ray cells usually similar, rarely elongated and simple, members of medium length. **Parenchyma** usually predominantly paratracheal in the Polygaleae, scanty or, less commonly, aliform or confluent; predominantly apotracheal, diffuse or banded, in the Moutabeae and Xanthophylleae. **Rays** typically exclusively uniseriate or up to 2 or 3 cells wide, but occasionally wider; heterogeneous. **Fibres** with bordered pits, of medium length to moderately short. **Included phloem** of the 'concentric' type present in the climbers.

LEAF

Hairs almost exclusively unicellular, but sometimes becoming uniseriate by septation in *Bredemeyera* and *Xanthophyllum*. Unicellular hairs with thick-walled apices recorded by Holm (1001, 1018) in *Polygala senega* Linn. Structure of the **mesophyll** very varied. (i) Consisting of one uniform tissue in a few species of *Mundtia* and *Carpolobia*. (ii) Leaves generally dorsiventral both in species with a relatively broad lamina, as well as in some of those which are lanceolate or linear with incurved margins. (iii) Centric in a few species of *Comesperma* (*Bredemeyera*), *Muraltia*, and *Polygala* possessing lanceolate or linear leaves with the margins incurved. Palisade parenchyma with folded lateral walls, and spongy parenchyma partly sclerosed in *Monnina speciosa* Tr. et Planch. Bundles of diamond-shaped bodies stated by Sabnis (1920) to be present in the palisade cells of *Polygala erioptera* DC. Cells of the **epidermis** generally with straight anticlinal walls except in a few species mentioned by Solereder; those on the lower surface provided with knob-like papillae in species of *Securidaca*, or sometimes with much thickened papillae in *Muraltia* and *Polygala*. Outer wall of epidermal cells sometimes strongly thickened. **Cuticle** smooth or with granular thickening; rarely striated. **Hypoderm** recorded only in *Moutabea guianensis* Aubl. Long sclerosed cells occur in the palisade tissue of the same species. **Stomata** present on both

surfaces or confined to the lower side, this difference being only of specific diagnostic value; generally ranunculaceous, but rubiaceous in certain species of *Securidaca* and *Xanthophyllum*. Stomata absent from the scale leaves of the saprophytic genus *Epirrhizanthus* (*Salomonina*). Vascular bundles of the **veins** of species with small leaves not generally accompanied by sclerenchyma. Veins vertically transcurrent in *Phlebotaenia* sp. Midrib usually with a single band or horseshoe-shaped vascular bundle, except in *Moutabea* with two strands, the upper one inversely orientated. **Petiole**, in transverse sections through the distal end, nearly always exhibiting a single, usually crescent-shaped bundle, e.g. in *Barnhartia floribunda* Gleason (Fig. 32 B), but with an almost completely closed vascular ring in *Bredemeyera*, *Polygala*, and *Securidaca*, or a completely closed ring in *Carpolobia*, *Moutabea* (Fig. 32 G), and certain species of *Xanthophyllum*. Mostly solitary but sometimes clustered **crystals** usually present in the leaf and axis, but none recorded in *Bredemeyera* and *Xanthophyllum*. Numerous **lysigenous cavities** recorded by Sabnis (1977) in the mesophyll towards the lower side of the leaf in *Polygala erioptera* DC. Oil drops and **oil ducts** stated by Holm (1918) to occur in certain North American species of *Polygala*, but not in other species of this genus from the same part of the world.

AXIS

YOUNG STEM (Fig. 32 H-I)

Epidermis strongly thickened in xerophilous species, but thin-walled in species having leaves adpressed to the stem; cells sometimes divided horizontally in *Securidaca*, and, according to Holm (1918), containing oil drops in certain species of *Polygala*. Primary **cortex** frequently collenchymatous, but containing stone cells in species of *Atroxima*, *Barnhartia*, *Carpolobia*, *Moutabea*, *Polygala*; strands of fibres also present in the cortex of herbaceous shoots of *Comesperma* and *Securidaca*, as well as in the ribs on the stems in certain species of *Comesperma* and *Polygala*. Palisade chlorenchyma recorded by Sabnis (1977) in certain species of *Polygala*. **Endodermis** indistinctly visible in *Polygala senega* Linn. but not seen by Holm (1918) in other North American species of this genus. **Pericycle** generally containing fibres either in the form of strands or as a continuous ring; their distribution varying considerably in different species of the single genus *Polygala*. The vascular cylinder is also surrounded by fibres in the saprophytic genus *Epirrhizanthus* (*Salomonina*). **Xylem**, in transverse sections, generally appearing as a closed ring in herbaceous species. Five primary collateral bundles, which subsequently become connected by cambium but without vessels arising in the interfascicular region, present in certain North American species of *Polygala*. Vessels usually small, sparse, and often scattered in the older wood of young stems, perforations simple. More numerous, spirally thickened vessels present in the protoxylem of species of *Moutabea*, *Securidaca*, *Swertia*. Solitary **crystals** observed in the cortex and/or phloem of species of *Atroxima*, *Barnhartia*, *Moutabea*, *Securidaca*. Clustered crystals observed only in the primary cortex of *Polygala oppositifolia* Linn. but possibly occurring elsewhere as well. Lysigenous oil ducts recorded by Holm (1918) in the cortex of certain North American species of *Polygala*.

WOOD (Fig. 33 and 91 B)

Vessels usually small to medium-sized ($60\text{--}150\mu$ mean tangential diameter) in most genera, large (more than 200μ) in some species of *Securidaca* and *Xanthophyllum*, and sometimes very to extremely small in small stems and twigs; typically exclusively solitary or nearly so, but in short multiples in *Bredemeyera* p.p. and in 'pore chains' in *Monnina* (938) and with some clusters in *Monnina* (938) and *Phlebotaenia*; usually about 7–12 per sq. mm., but fewer than 5 per sq. mm. in some species of *Securidaca* and *Xanthophyllum*; spiral thickening observed in *Mundtia spinosa* DC. and recorded by Solereder for *Polygala eckloniana* Presl. and *Muraltia ononidifolia* Eckl. et Zeyh. Perforations simple, transverse or slightly oblique; Heimsch (938) notes a few net-like plates in one species of *Polygala*. Intervascular pitting rare in genera with solitary vessels, alternate, moderate-sized to small, and minute in some species of *Xanthophyllum*; pits to ray cells similar to the intervacular pitting in most genera, but in *Carpolobia* p.p. and *Moutabea* (938) small bordered pits are accompanied by relatively large, circular or oblong pits with narrow borders or simple. With a few sclerotic tyloses in *Moutabea* (938). Mean member length 0.4–0.5 mm. **Parenchyma** predominantly paratracheal in *Badiera*, *Bredemeyera*, *Carpolobia*, *Monnina*, *Mundtia*, *Phlebotaenia*, *Polygala*, and *Securidaca* p.p.; usually scanty and limited to a few cells round the vessels, but tending to be aliform in some species of *Bredemeyera* and *Carpolobia*, e.g. in *C. goetzei* Gürke, aliform to confluent in *Phlebotaenia*, and as long uniseriate wings attached to the vessels on the abaxial sides in *Carpolobia parvifolia* Stapf f. (Fig. 33 E). Some diffuse parenchyma may occur in addition in *Phlebotaenia* and *Securinaga* and in the latter predominates in some species. According to Heimsch (938), however, the parenchyma in *Carpolobia* and *Polygala* is diffuse, and, according to Record and Hess (1886), that of *Monnina* is irregularly diffuse and terminal. Apotracheal parenchyma appears to be characteristic of *Moutabea* and *Xanthophyllum*, diffuse in the former and in broken to continuous uniseriate bands in the latter (Fig. 33 F). Chambered crystalliferous strands present in *Carpolobia* and *Phlebotaenia*. Parenchyma strands usually of 4 cells, but commonly of 8 cells in *Xanthophyllum*. **Rays** exclusively uniseriate, or only occasionally biseriate (Fig. 32 A, C, and G), in some species of *Bredemeyera* (twigs of *B. lucida* A. W. Benn.), *Carpolobia*, *Mundtia*, *Phlebotaenia*, *Securidaca*, and *Xanthophyllum*; up to 2 or 3 cells wide in the other genera and in *Securidaca* p.p., but with occasional larger rays in the latter and with rays up to 5 or 6 cells wide in *Monnina* (1886) and *Moutabea* (938); usually low, but sometimes more than 1 mm. high in *Xanthophyllum*; uniseriates numerous in species with multiseriata rays, and usually composed of procumbent and upright cells; usually 11–19 rays per mm.; heterogeneous (Kribs's Types II A and B and III), sometimes with 4 or more uniseriate rows of erect marginal cells; the 'procumbent' cells sometimes almost square and occasionally, e.g. in *Securidaca*, with square and upright cells only. **Fibres** with distinctly bordered pits that are equally numerous in both radial and tangential walls, the borders of about the same size as those of the intervacular pitting. Walls moderately thin to thick. Mean length 0.8–1.1 mm. Vasicentric **tracheids** present in *Securidaca*. **Included (interxylary) phloem** of the 'concentric' type (*c. l. circumvallatum*) present in species of *Bredemeyera* (1886), *Moutabea* (1886),

and *Securidaca*. Successive layers or arcs of xylem and phloem repeating the structure of the young stem are separated by rather broad tangential bands of conjunctive parenchyma (Fig. 91 B); the conjunctive tissue is unligified and often includes a band of cells similar to pericyclic fibres (Fig. 33 B); xylem layers seldom interrupted by interfascicular rays.

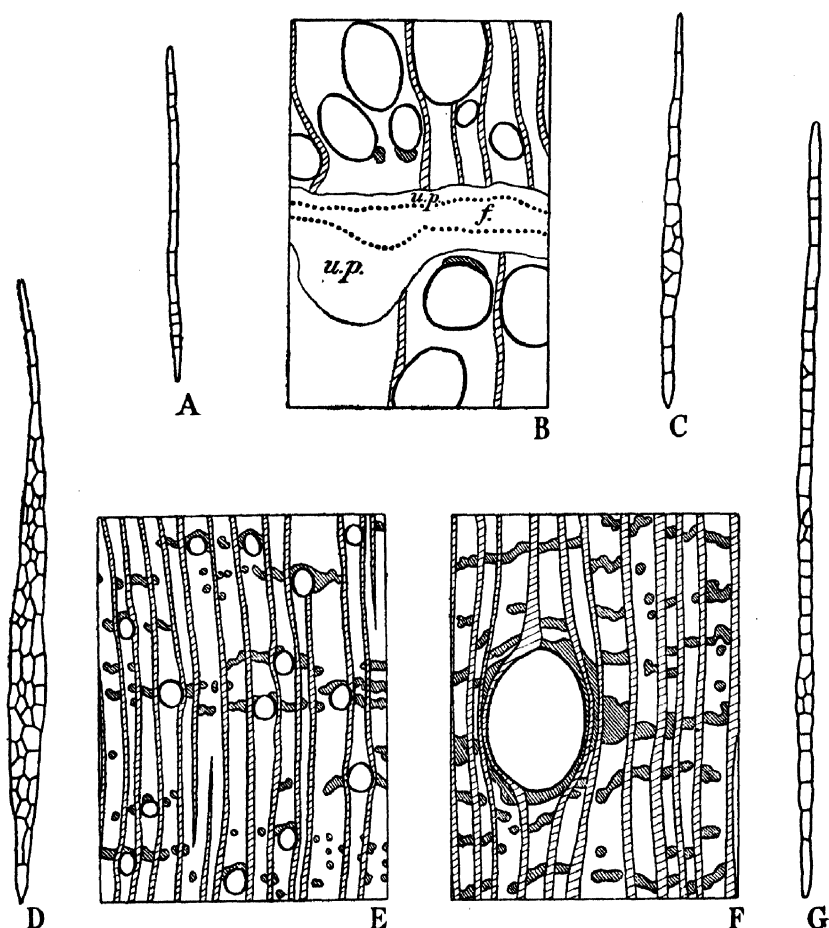


FIG. 33. POLYGALACEAE

A, *Carpolobia parvifolia* Stapf f. B, *Securidaca diversifolia* (L.) Blake. C, *S. virgata* Sw. D, *S. longipedunculata* Fresn. E, *Carpolobia parvifolia* Stapf f. F, *Xanthophyllum affine* Korth. G, *X. affine* Korth.

f. Cells resembling pericyclic fibres. u.p. Unligified parenchyma.

ANOMALOUS STRUCTURE, see under 'WOOD'

ROOT

Thin lateral roots of *Polygala lutea* Linn. stated to be devoid of hairs, but provided with a papillose epidermis. The root of *Polygala senega* Linn. is described under 'Economic Uses'.

TAXONOMIC NOTES

Krameria. Heimsch (938) has shown that, in its wood anatomy, *Krameria* differs markedly from the Leguminosae, but would not be out of place in the Polygalaceae. See also under 'Krameriaceae', p. 538.

Diclidanthera. O'Donnell (1630), in a study of the pollen grain morphology and wood anatomy of *Diclidanthera*, concludes that this genus belongs to the Polygalaceae. Unpublished work by Sprague and Metcalfe also supports this view that *Diclidanthera* is related to the Polygalaceae. See also under 'Diclidantheraceae', p. 138.

Xanthophyllum. This genus differs in its wood parenchyma from all the other members of the Polygalaceae; this would tend to support the treatment of this genus as a monotypic family. Jauch (1157), on the other hand, considers that *Xanthophyllum* should be retained in the Polygalaceae, this opinion being based on the evidence of floral anatomy and the structure of pollen grains.

Heimsch (938) considers the wood anatomy to show that the Polygalaceae form part of an interrelated group, the other members of which are the Trigoniaceae, Tremandraceae, Zygophyllaceae, Malpighiaceae, and Vochoysiaceae, and that, though they are more specialized in their wood structure, these families are generally related to the Linaceae, Humiriaceae, and Erythroxylaceae.

Jauch (1157) suggests that the occurrence of lysigenous canals in certain American species indicates a possible affinity between the Polygalaceae and Anacardiaceae.

ECONOMIC USES

Senega or Snake Root, imported from South Canada and the U.S.A. for medicinal use, is derived from *Polygala senega* Linn. Certain Indian species of *Polygala* also possess roots with medicinal properties (see 'Root' above). A fibre is obtained in East Africa from *Securidaca longipedunculata* Fres. The following anatomical features of *Polygala senega* have been recorded by Holm (1018), Steiger (2191), and in the *British Pharmaceutical Codex*. Young roots normal in structure, but becoming eccentric and sometimes winged when mature. Epidermis sparingly hairy. Some of the cells of the cortex containing a yellowish substance. Endodermis thin-walled. Cork in older roots formed from the cambium, the primary cortex and endodermis then becoming disorganized. The secondary cortex also originating from the cambium, frequently very unequally developed; instances being recorded of its consisting of 20 layers of cells on one side of the root and only 10 on the other. Secondary xylem and phloem present in the form of collateral bundles. Small strands of phloem also occur in the cortex at some distance from the main stele. The xylem consists of numerous pitted tracheids and less frequent smaller vessels, the latter often containing a yellowish oily substance. Rays long and narrow on one side of the root, but short and broad on the other. Parenchyma of the root containing oil but no starch. Fibres and calcium oxalate crystals absent.

Commercial samples of Indian Senega root submitted to Kew for identification differed from the American species in having abundant cells with brown contents in the inner part of the cortex. On another occasion a

substitute for *Polygala senega* was received from the Middle East. This sample showed a succession of interrupted concentric rings of xylem and phloem situated externally to the central xylem mass. Although this type of structure is known in other members of the family it has never been definitely recorded in *Polygala* itself, but Holm (1918) implies that it may sometimes occur in this genus also. A specimen with the same structure as that of the Middle East sample was found as an admixture in a sample of *P. serpentaria* from South Africa.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Atroxima,* Barnhartia,* Bredemeyera, Carpolobia,* Epirrhizanthus (Salomonina), Monnina, Moutabea,* Mundtia, Muraltia, Phlebotaenia, Polygala,* Securidaca,* Xanthophyllum.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Badiera, Bredemeyera, Carpolobia, (Monnina), (Moutabea), Mundtia, (Muraltia), Phlebotaenia, Polygala, Securidaca, Xanthophyllum.

LITERATURE

(i) On General Anatomy

Holm 1901, 1918, Jauch 1157, O'Donell 1630, Sabnis 1977, Steiger 2191.

(ii) On Wood Structure

den Berger 179, Chalk and Chattaway 362, Cooper 461, Heimsch 938, Lecomte 1334, O'Donell 1630, Pfeiffer, H. 1711, 1712, Record 1843, 1851, Record and Hess 1886.

38. DICLIDANTHERACEAE

SUMMARY

The anatomy of the Brazilian shrubs and trees belonging to the genus *Diclidanthera* is rather imperfectly known. The following facts concerning *D. laurifolia* Mart. have been recorded by Solereder and those concerning *D. penduliflora* Mart. observed at Kew. The wood exhibits the following features. **Vessels** mostly solitary, with simple perforations and alternate intervacular pitting. Vasicentric **parenchyma**. Wide, heterogeneous **rays**. **Fibres** with bordered pits.

LEAF

Dorsiventral. **Hairs** in *D. laurifolia* Mart. simple, with thin septa. **Hypoderm** of 1-2 layers of large cells well developed below the upper epidermis. **Mesophyll** of *D. penduliflora* Mart. including about 3 layers of palisade tissue. **Midrib**, in the same species, containing a single vascular bundle, strongly supported on the abaxial and to a smaller extent on the adaxial side by thick-walled fibres. Vascular bundles of the **veins**, again in the same species, embedded in the mesophyll and entirely sheathed by thick-walled fibres. Solitary **crystals** in both species, numerous in cells adjacent to the vascular bundles.

AXIS

YOUNG STEM

Cork in *D. laurifolia* Mart. arising superficially; said to be composed of stone cells. **Pericycle** in both *D. laurifolia* Mart. and *D. penduliflora* Mart. including a broad, continuous, composite ring of sclerenchyma. Secondary **phloem** said to include pitted, sclerenchymatous elements in *D. laurifolia*, but no sclerosed elements observed in the phloem of young twigs of *D. penduliflora*. **Xylem** in *D. penduliflora* appearing, in transverse sections, as a continuous cylinder traversed by narrow, mostly uniseriate medullary rays. Vessels, in the same species, somewhat unevenly distributed being entirely absent from some segments of the xylem, mostly solitary, but some in tangential or oblique pairs or clustered; only simple perforations known to occur. **Pith** fairly broad in *D. penduliflora*; consisting of moderately thick-walled, pitted cells. Stone cells recorded in the pith of *D. laurifolia*.

WOOD¹

Vessels mostly solitary, perforations simple, intervacular pitting alternate. **Parenchyma** vasicentric. **Rays** tending to break up into smaller units; heterogeneous (Kribs's Type II A-B). **Fibres** with large bordered pits.

TAXONOMIC NOTES

The taxonomic position of *Diclidanthera* is not well established. The anatomical features, so far as they have been studied, tend to support the unpublished view put forward by Dr. T. A. Sprague that *Diclidanthera* may have affinities with the Polygalaceae. O'Donell (1930) concludes from a study of the anatomy, and particularly of the anomalous secondary thickening, that *Diclidanthera* should be in the Polygalaceae near *Moutabea* and *Securidaca*.

GENUS DESCRIBED

Diclidanthera.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy and Wood Structure
O'Donell 1930.

39. VOCHYSIACEAE

(FIG. 34 on p. 144)

SUMMARY

(i) GENERAL

A small family, including large trees, shrubs, and climbers. It occurs chiefly in tropical America but extends to West Africa. **Hairs** exclusively non-glandular; always unicellular but sometimes tufted, e.g. in *Erisma*. Large **nectaries** have been recorded above the stipules in species of *Qualea*. The **stomata** are said to be ranunculaceous in *Erisma*, *Salvertia*, *Vochysia*, and rubiaceous in *Qualea*. The **epidermis** of the leaf is frequently composed of

¹ Based entirely on the description by O'Donell (1930).

cells with mucilaginous inner walls. In the stem, **cork** arises in the outer part of the cortex in *Salvertia* and *Vochysia* and in the pericycle in *Erismia* and *Qualea*. **Intraxylary phloem** occurs in the form of a ring or as separate strands in the perimedullary region, whilst in some species a ring and separate strands occur together. Solitary **crystals** have been reported in *Erismia* and *Qualea* and clustered ones in *Callisthene*, *Salvertia*, and *Vochysia*. **Secretory elements**. Mucilage cells occur in the cortex and pith of *Qualea*, and mucilage canals in the pith of the stem and petiole as well as in the leaf veins in *Erismia*, *Salvertia*, *Vochysia*.

(ii) WOOD

Vessels medium-sized to large and few, perforation plates simple, intervascular pitting alternate, pits to parenchyma similar or elongated, members of medium-length to moderately short. **Parenchyma** paratracheal, aliform and confluent, the latter often in broad continuous bands. **Rays** up to 2–8 (usually 3–5) cells wide, heterogeneous to homogeneous. **Fibres** with simple pits, occasionally septate, of medium length. Traumatic vertical **inter-cellular canals** moderately common. **Included phloem** of the ‘foraminate’ type sometimes present.

LEAF

Dorsiventral except in *Qualea glauca* Warm. where palisade tissue occurs towards both surfaces. **Hairs** mostly simple, unicellular, but varying in length and in the thickness of the walls, in *Callisthene*, *Qualea*, *Salvertia*, &c.; unicellular, 2-armed in certain species of *Vochysia*; tufted, and provided with a variable number of rays in *Erismia*. Glandular hairs absent. Solitary extrafloral **nectaries** recorded above the stipules in *Erismia laurifolium* Warm. and *Vochysia oppugnata* Warm. **Epidermis** on both surfaces composed of polygonal cells as seen in surface view; cells on the upper side in *Erismia violaceum* Mart. remarkably small and in part divided by thin, vertical secondary walls; 2-layered on the upper surface in certain species of *Qualea* and in *Vochysia rufa* Mart.; frequently mucilaginous, for example, in species of *Callisthene*, *Qualea*, *Salvertia*; cells of the lower epidermis papillose in *Qualea glauca* Warm. **Stomata** confined to the lower surface; ranunculaceous in at least certain species of *Erismia*, *Salvertia*, *Vochysia*; rubiaceous stomata recorded in *Callisthene* and *Qualea*. **Mesophyll** including spirally thickened storage tracheids in *Vochysia rufa* Mart. Vascular bundles of the smaller **veins** vertically transcurrent by thin-walled or, less frequently, by sclerotic cells. Vascular bundles in large and small veins with or without an investment of sclerenchyma according to the species. Only solitary **crystals** recorded in *Erismia* and *Qualea* and clustered ones in species of *Callisthene*, *Salvertia*, *Vochysia*. **Secretory elements**. Mucilage cells present in the parenchymatous portions of the petiole in various species of *Qualea*, and mucilage canals in the petiole and veins of species of *Erismia*, *Salvertia*, *Vochysia*.

AXIS

YOUNG STEM

Cork arising in the outer part of the cortex in *Salvertia* and *Vochysia* and in the pericycle in *Erismia* and *Qualea*. **Cortex** containing abundant scleren-

chyma. **Pericycle** also including sclerenchyma, that of *Qualea glaziovii* Warm. forming an almost closed ring. **Pith** including groups of sclerenchyma in species of *Erisma*, *Qualea*, *Salvertia*, *Vochysia*. **Intraxylary phloem** recorded in 29 species included in the genera *Callisthene*, *Erisma*, *Qualea*, *Salvertia*, *Vochysia*; in the form of strands in species of *Erisma*, *Salvertia*, and *Vochysia*; constituting a continuous ring in the outer part of the pith in *Callisthene* and *Qualea*; a continuous ring accompanied by separate strands noted in species of *Erisma* and *Qualea*. For **Interxylary phloem** see under 'Wood'. **Secretory elements**. Mucilage cells common in the pith and cortex of *Qualea*. Mucilage canals in the pith recorded in *Erisma micranthum* Spruce, *Salvertia convallariaeodora* St. Hil. and numerous species of *Vochysia*. Tannin cells said to be widely distributed in the pith and cortex.

WOOD (Fig. 34 C-G)

Vessels medium-sized (100–200 μ mean tangential diameter) to large (more than 200 μ) in some species of *Qualea* and *Vochysia*; solitary and in radial multiples of 1–4 cells; usually about 2 per sq. mm. Perforations simple, transverse or slightly oblique. Intervascular pitting alternate and vested (78), in *Erisma* medium-sized to rather large and pits to ray cells often oblong and simple or with only very narrow borders; intervacular pitting rather small and with pits to ray cells similar in *Qualea* and *Vochysia*. Tyloses and solid white deposits sometimes present. Mean member length 0.3–0.7 mm. **Parenchyma** predominantly paratracheal, aliform and confluent in all three genera; the confluent parenchyma forming regular, continuous bands 2–6 cells wide in *Erisma* and *Vochysia* (Fig. 34 D and E) and rather less continuous bands in *Salvertia* (Heimsch 938); usually with a few cells or groups of cells scattered among the fibres. According to Heimsch (938) the parenchyma and vessels in *Qualea grandiflora* Martius together form an irregular, diagonal reticulum. Occasionally containing chambered crystals in *Erisma* and *Qualea*. Strands most commonly of 4 cells. **Rays** most commonly up to 3–5 cells wide, but a few rays up to 6–8 cells wide in some species of *Vochysia*; up to 1 mm. high in *Vochysia hondurensis* Sprague, but typically lower; uniseriate numerous in *Erisma* and *Vochysia* and composed of upright cells, rather few and composed of procumbent and upright cells in *Qualea*; about 5–8 rays per mm.; heterogeneous (Kribs's Type II A and B) in *Erisma* and *Vochysia*, with up to 3 or 4 uniseriate marginal rows of square and upright cells; almost or quite homogeneous (Kribs's Type Het. II B–Hom. I) in *Qualea*. **Fibres** with few, small, simple pits that are almost confined to the radial walls; the pits sometimes with very small borders in *Vochysia*; a few cells sometimes septate in *Erisma* and *Vochysia* (1894). Mean length 1.0–1.3 mm. **Intercellular canals** of the vertical traumatic type observed or reported in *Erisma* (1712), *Qualea* (1801) and *Vochysia* (Fig. 34 G). **Included (interxylary) phloem** of the 'foraminate' type common in *Erisma* (1712) and reported in *Erismadelphus* (1851) and *Qualea* (1886), though rare in the latter; consisting of strands of unligified phloem scattered through the wood, surrounded and often linked together by parenchyma (Fig. 34 E); strands of what appears to be soft bast (Fig. 34 F) commonly present also in the rays of *Erisma* (362).

ANOMALOUS STRUCTURE, *see under* 'WOOD'

TAXONOMIC NOTES

Heimsch (938) considers that in its wood anatomy this family forms part of an interrelated group, the other members of which are the Polygalaceae, Trigoniaceae, Tremandraceae, Zygophyllaceae, and Malpighiaceae, but notes that the Malpighiaceae and Vochysiaceae differ from this complex in having libriform fibres and vested pits; the Vochysiaceae are further set apart by the pronounced development of banded parenchyma and the occurrence of intercellular canals.

ECONOMIC USES

The timbers generally appear to be of little commercial importance, but Ymeri, *Vochysia hondurensis* Sprague, from British Honduras shows some promise as a plywood and for purposes similar to those for which Gaboon Mahogany is used.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Callisthene, Erisma, Qualea, Salvertia, Vochysia.

(ii) FOR WOOD STRUCTURE

Erisma, (Erismadelphus), Qualea, (Salvertia), Vochysia.

LITERATURE

On Wood Structure

Bailey 78, Benoist 170, Besson 186, Campbell 2514, Chalk and Chattaway 362, Heimsch 938, Howard 1088, Kanchira 1209, Kribs 1283, Mériaud 1491, Pfeiffer, H. 1712, Record 1787, 1801, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2207, Williams, L. 2530.

40. TRIGONIACEAE

(FIG. 34 on p. 144)

SUMMARY

(i) GENERAL

A small family of trees and climbing shrubs which occur in tropical South America. The **hairs** are exclusively simple and unicellular. The **epidermis** of the leaf is frequently composed of cells with mucilaginous inner walls. The **stomata** in *Trigonia* are commonly rubiaceous. In the young stem the **cork** arises in the outer part of the cortex. The **vascular bundles** are simple, collateral, whilst the xylem includes vessels with simple perforations embedded in prosenchymatous ground tissue with bordered pits. The family differs from the *Vochysiaceae* in the absence of **intraxylary phloem**.

(ii) WOOD

Vessels solitary, perforations simple, members moderately long. **Parenchyma** apotracheal (diffuse and banded) or paratracheal (aliform). **Rays** up to 4 cells wide, uniseriatae moderately numerous, heterogeneous with many marginal rows. **Fibres** with bordered pits, of medium length.

LEAF

Dorsiventral. **Hairs**; only simple, unicellular types known. **Epidermis** often consisting of mucilaginous cells, the latter being polygonal in surface view; those of *Lightia licanoides* Spruce specially small. Epidermis partly or wholly 2-layered in *Lightia licanoides* and *Trigoniastrum hypoleucum* Miq. A large-celled, mucilaginous **hypoderm** also recorded in the first of these species. **Stomata** confined to the lower surface in all investigated species; commonly rubiaceous in *Trigonia*. **Mesophyll** including branched sclerenchymatous fibres in *Lightia licanoides* and *Trigoniastrum hypoleucum*. Vascular bundles of the **veins** with or without an investment of sclerenchyma according to the species. **Crystals** of calcium oxalate solitary or clustered.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis. Secondary **phloem** containing sclerenchyma. **Xylem** consisting of a cylinder traversed by rays 3–5 cells wide, and including vessels with simple perforations embedded in prosenchymatous ground tissue with bordered pits. **Intraxylary phloem** absent. Solereder reports Petersen as having recorded the occurrence of inversely orientated **medullary bundles** in an undetermined species of *Trigonia*.

WOOD (Fig. 34 A–B)

Vessels usually exclusively solitary, but Heimsch (938) notes some pore multiples in *Trigonia*. Perforations simple; Heimsch has observed some vestigial scalariform plates in *Trigonia*. Intervascular pitting extremely rare; pits to parenchyma and ray cells alternate and rather small or large and elongated. Mean member length (*Trigoniastrum*) 0.9 mm. **Parenchyma** in *Trigoniastrum* apotracheal,¹ diffuse and in short tangential lines; sometimes with some paratracheal in addition (Fig. 34 A); similar or with distinct apotracheal bands in *Trigonia*; paratracheal in *Lightia*, vasicentric or 'abaxial, with or without aliform extensions which may connect as many as four or five vessels' (938). Sometimes containing chambered crystals. Strands commonly of 8–12 cells in *Trigoniastrum*. **Rays** up to 4 cells wide; uniseriate moderately numerous and composed of upright cells or mixed procumbent, square and upright cells; heterogeneous (Kribs's Type II A and B), sometimes with many uniseriate marginal rows, and varying in different species from mostly procumbent to square and seldom upright, to all square or upright. Sometimes containing chambered crystals. Heimsch (938) notes spiral and reticulate thickening in the ray and wood parenchyma cells of *Trigonia sericea* H. B. et K. **Fibres** with distinctly bordered pits in both radial and tangential walls. Heimsch refers to septate elements as occurring in some species. Walls usually thick. Mean length (*Trigoniastrum*) 1.3 mm.

TAXONOMIC NOTES

The Trigoniaceae were, in the Bentham and Hooker system, included in the Vochysiaceae, from which they differ most conspicuously in the absence

¹ A single specimen of *Trigoniastrum hypoleucum* Miq. from Java differed from the other material of this genus examined or described in having paratracheal parenchyma similar to that described below for *Lightia*.

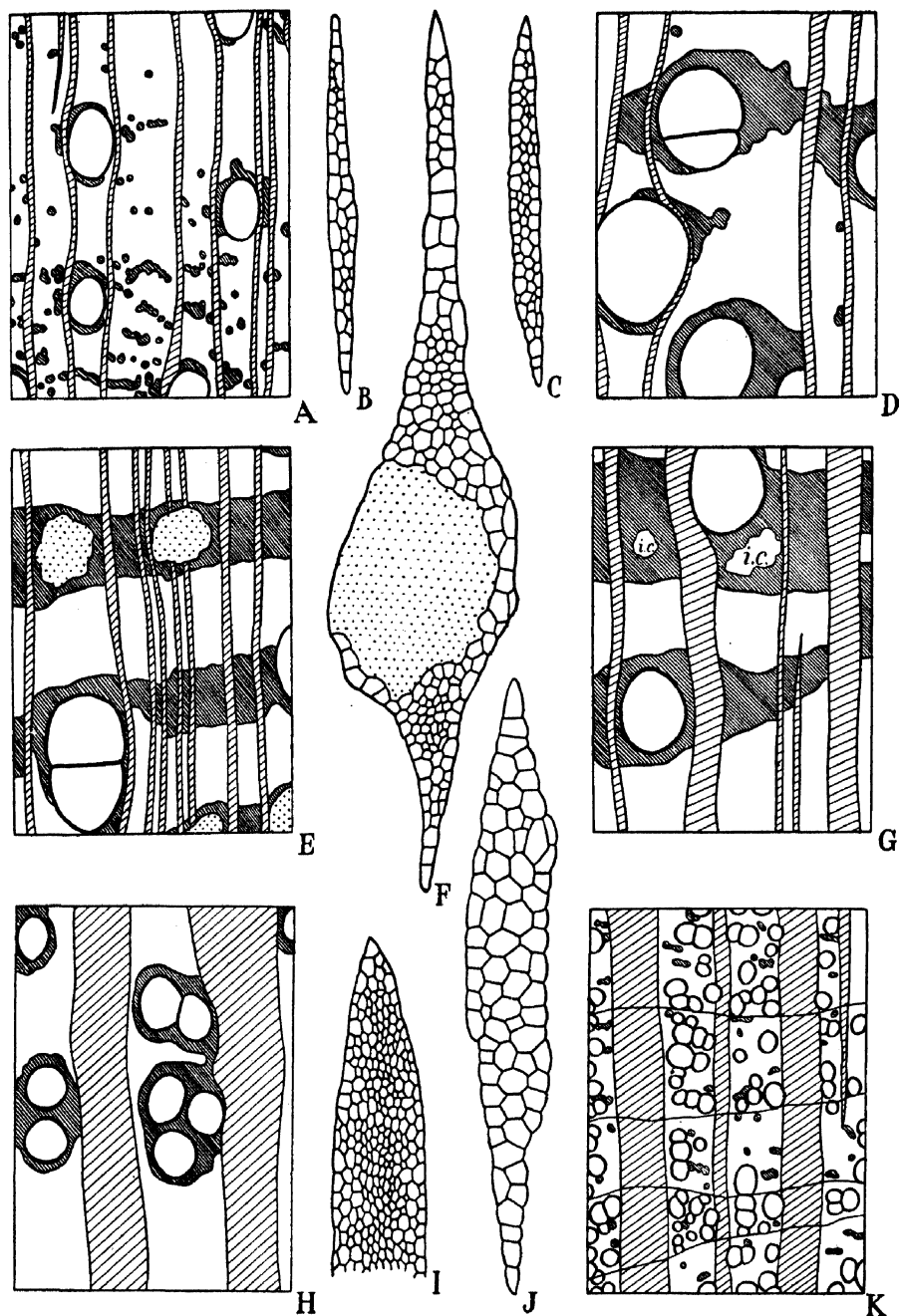


FIG. 34. *TRIGONIACEAE*, A-B; *VOCHYSIACEAE*, C-G; *TAMARICACEAE*, H-I; *FOUQUIERACEAE*, J-K

A, *Trigonistrum hypoleucum* Miq. B, *T. hypoleucum* Miq. C, *Qualea rosea* Aubl. D, *Q. rosea* Aubl. E, *Erisma bicolor* Ducke. F, *E. bicolor* Ducke. G, *Vochysia hondurensis* Sprague. H, *Tamarix articulata* Vahl. I, *T. mannifera* Ehr. J, *Fouquieria splendens* Engelm. K, *F. splendens* Engelm.
i.c. Intercellular canals.

of intraxylary phloem and in having bordered pits to the ground tissue elements of the xylem.

Heimsch (938), on the basis of the wood anatomy, groups this family with the Polygalaceae, Tremandraceae, Zygophyllaceae, Malpighiaceae, and Vochysiaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Lightia, Trigonía, Trigoníastrum.

(ii) FOR WOOD STRUCTURE

(Lightia), (Trigonía), Trigoníastrum.

LITERATURE

On Wood Structure

Heimsch 938, Record 1843, 1851, Record and Hess 1886.

41. FRANKENIACEAE

(FIG. 32 on p. 130; FIG. 35 on p. 146)

SUMMARY

Herbs or shrublets, mostly from maritime regions or dry areas such as steppes and deserts. They exhibit ecological specializations in correlation with these habitats, such as leaves with revolute margins, or ericoid microphylls which are sometimes adpressed to the stem. The structure of the mesophyll is largely determined by the morphology and orientation of the leaves. The most distinctive anatomical character is the universal occurrence of **epidermal salt glands** of a special type (Fig. 35 A-C), generally situated in pits. They consist of about 6 cells derived from the division of a single epidermal cell, the 2 uppermost cells resembling a pair of guard cells as seen in surface view. **Hairs** are simple trichomes, generally unicellular but sometimes tufted. Calcium oxalate is known to occur only in the form of clustered **crystals**. **Cork** in the stem is sub-epidermal in origin in all of the genera except *Anthobryum*. The **phloem** consists of very small elements. The **xylem** contains vessels with very narrow lumina, and definite medullary rays are lacking. The **pith** consists of large cells in young stems, but becomes hollow when older.

LEAF

Generally dorsiventral in species with revolute margins, but tending to be sub-centric in *Frankenia portulacifolia* Beatson (syn. *Beatsonia portulacoides* Roxb.) and certain other species of *Frankenia*. The shape of transverse sections of the leaf taken at corresponding levels is valuable for the identification of species. Half the thickness of the **mesophyll** in species with dorsiventral leaves consists of palisade tissue, but palisade tissue develops only towards the lower surface in species with the upper surface adpressed to the axis. Intermediate types of mesophyll with a certain amount of palisade tissue towards both surfaces also recorded in some species of *Frankenia*, or

consisting wholly of palisade cells in other species such as *F. corymbosa* Desf. **Hairs** mostly simple, unicellular, sometimes tufted; either thin- or thick-walled; in some instances having the form of papillae, but in others considerably longer. Some of the hairs bicellular and/or paired in *Frankenia portulacifolia* Beatson. **Epidermal glands** (see 'Summary') sometimes paired in *Niederleinia*. **Cuticle** often thick, especially in *Niederleinia*. Cells of the **epidermis** frequently enlarged. **Stomata** ranunculaceous; usually sunken; in some species confined to grooves.

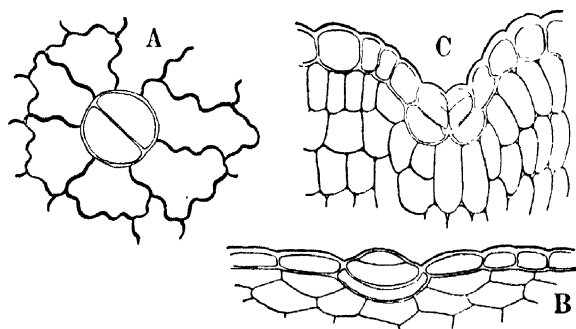


FIG. 35. FRANKENIACEAE

Gland of *Frankenia pulverulenta* L.: A, In surface-view. B, In a section cut parallel to the common vertical wall of the 2 gland-cells. C, In a section cut perpendicularly to this vertical wall.—By Solereder.

Variations in the nature and distribution of the **mechanical tissue** stated by Niedenzu (1596) to provide a reliable means for identifying species which are not readily distinguished by floral characters. Sclerenchyma more or less well developed in the phloem in *F. thymifolia* Desf., *F. jamesii* Torr., and *Niederleinia*; vascular bundles accompanied by a sclerenchymatous sheath in the *Basigonia* section of *Frankenia*; mechanical elements consisting of 'spicular cells' (i.e. bundles of branched sclerenchymatous cells around the veins) in *F. bracteata* Turcz., &c., or of thick-walled xylem elements in *F. campestris* Schau., &c. Certain of the palisade cells become thick-walled and serve a mechanical function in *F. portulacifolia* Beatson. Principal **veins** embedded in the mesophyll; variations in their number and degree of development said to be a feature of specific diagnostic value. The median vein alone well developed in *Hypericopsis persica* (Jaub. et Spach) Boiss. and *Niederleinia juniperoides* Hieron. although smaller subsidiary bundles also occur in the upper part of the leaf sheath of *Niederleinia*, and larger ones in *Anthobryum*. Vascular bundles of the veins made up of xylem containing vessels with narrow lumina and phloem composed of very small elements. **Petiole** in *Hypericopsis* described by Surgis (2222) as exhibiting a similar vascular structure to that of the median vein of the lamina.

AXIS

YOUNG STEM (Fig. 32 A)

The following features may be added to those given in the summary.

Epidermis narrow, without hairs, glands, or stomata in *Niederleinia*, but

according to Surgis (2222) possessing all of these structures in *Hypericopsis*. **Cork** pericyclic in origin in *Anthobryum*. **Pericycle** containing rings of fibres in *Hypericopsis*; seen to include strands of fibres in *Frankenia laevis* Linn. when examined at Kew (Fig. 32 A), but a composite continuous ring of sclerenchyma also recorded in the same species. **Phloem** and **xylem** in the form of continuous cylinders in *F. laevis*. Vessels of the **xylem** in all species small, scattered, with simple perforations; those of *F. laevis* up to about $30\ \mu$ in radial diameter. Ground tissue of the xylem composed of prosenchyma with simple pits.

(Surgis (2222) gives particulars of anatomical characters whereby individual species in this family may be recognized. These can best be consulted in his paper.)

ECONOMIC USES

Frankenia portulacifolia Beatson (syn. *Beatsonia portulacoides* Roxb.) is the source of St. Helena tea.

TAXONOMIC NOTES

The family is well defined by the possession of characteristic epidermal glands, but it is interesting to note that similar glands also occur in the Tamaricaceae and Plumbaginaceae. The glands are probably to be regarded as an ecological specialization which may quite well have arisen independently in each of these families. Other families to which it has been suggested that the Frankeniaceae may be related include the Elatinaceae and Caryophyllaceae. The anatomical structure of *Anthobryum* confirms that this genus belongs to the Frankeniaceae and not to the Primulaceae in which it was at one time included.

GENERA DESCRIBED

Anthobryum, *Beatsonia*, *Frankenia*,* *Hypericopsis*, *Niederleinia*.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Niedenzu 1596, Surgis 2222.

42. CARYOPHYLLACEAE

(Including *Illecebraceae* of *Bentham and Hooker*)

(FIG. 37 on p. 154; FIG. 38 on p. 160)

SUMMARY

A family of annual or perennial herbs, most of which have a number of anatomical characters in common. It occurs chiefly in north temperate regions, but some species extend far to the north. The **hairs** are generally simple, unicellular or uniseriate trichomes, sometimes provided with a unicellular glandular head. Branched hairs also occur in certain genera (see 'Leaf'). **Stomata** are usually of the so-called caryophyllaceous type, being accompanied by 2 subsidiary cells whose common wall is placed transversely to the pore, but exceptions occur, especially amongst the genera included by

Bentham and Hooker in the Illecebraceae. Even amongst these the caryophyllaceous type of stoma also occurs in *Habrosia* and *Scleranthus*. The leaf may be dorsiventral or centric, whilst an interesting feature of certain arctic species is that the palisade tissue is confined to the abaxial side. The amount and distribution of the palisade tissue sometimes varies within a species according to the nature of the illumination. Even arctic members of the genus exhibit no anatomical specializations which serve for the reduction of transpiration, a feature which Warming (2362) suggests is possibly correlated with the obliquity of the sun's rays which fail to raise the temperature of the leaves appreciably, whilst the atmospheric humidity is very great, fogs and cloud being frequent. In this connexion it is important to realize, however, that the cushion-like habit and common occurrence of narrow overlapping leaves may also be important. Calcium oxalate is commonly secreted in the form of large, conspicuous **cluster-crystals**, although solitary crystals and crystal-sand occur rarely. A narrow or broad ring of sclerenchyma is nearly always present outside the phloem. In some instances the prosenchymatous elements of which these rings are composed have much thicker walls, and the lumen is narrower towards the outside than in those towards the phloem. When this is so the prosenchymatous nature of the inner elements is not apparent in transverse sections, although their true nature is revealed in longitudinal sections. Solereder described these sclerenchyma rings as occurring in the cortex, but observations made at Kew suggest rather that they are pericyclic, the true primary cortex being very narrow in some instances. The **xylem** and **phloem** of the stem appear, in transverse sections, either in the form of a continuous cylinder, or as individually distinct bundles separated by broad rays. Intermediate conditions between these two types also occur. The arrangement of the vascular tissue appears to be characteristic for species and therefore of diagnostic value. Secondary medullary rays apparently do not occur. Vessels with simple perforations. **Anomalous secondary thickening**, consisting of the formation of successive rings of bundles, occurs in old stems, but more frequently in roots of certain genera. Friedel and Yen (719) have described an interesting species of *Drypis* which strongly resembles an *Eryngium* (Umbelliferae) in external form. They show nevertheless that the internal structure of the 2 genera differs considerably, that of the *Drypis* being strongly caryophyllaceous in type.

LEAF

Dorsiventral or centric; central tissue serving for water-storage in *Sphaerocarpos*. For further details see under 'Mesophyll' below. **Hairs**. (i) Unicellular types recorded in certain species of *Hermiaria*, *Paronychia*, *Siphonychia*. (ii) Simple, long or short, uniseriate hairs frequent in most genera except some of those included by Bentham and Hooker in the Illecebraceae. (iii) Uniseriate hairs with a glandular cell at the apex recorded in *Dysphania*, *Habrosia*, *Loeflingia*, *Silene* (Fig. 37 A), *Spergula*, *Spergularia*. Almost sessile glands (Fig. 37 B) occur, for example, in *Viscaria*. (iv) Branched hairs occur in *Achyronichia*, *Cerastium*, *Pollichia* sp., *Polycarpaea*, *Polycarpon*, and *Stipulicida*. Hair structure believed by Correns (476) to be of specific diagnostic value in *Cerastium*. **Epidermis** composed of cells with straight or undulating

anticlinal walls, cells elongated in species with long leaves. Epidermal cells especially tall as seen in transverse section in some species; papillose in certain species of *Gypsophila*, *Polycarpon*, and *Saponaria*, the nature of the papillae being of specific diagnostic value in the last of these. Papillae in longitudinal rows, chiefly near the midrib and margin in *Achyronychia*, *Cometes*, *Corrigiola*, *Habrosia*, *Loeflingia*, *Ortegaia*, *Pollichia*, *Polycarpaea*, *Polycarpon*, *Scleranthus*. **Cuticle** smooth, punctate or variously striated in different species. **Wax** thickly deposited on the surface in certain species of *Cometes*, *Dicheranthus*, and *Pteranthus*. **Stomata** generally of the caryophyllaceous type (Fig. 37 c and 38 b), but exceptions also recorded, notably in the Caryophyllaceae-Polycarpeae except *Loeflingia*, and Illecebraceae of Bentham and Hooker. The caryophyllaceous type of stoma is also rare in certain species of *Arenaria*, *Cerastium*, and *Stellaria* with elongated epidermal cells. Stomata sometimes tending to be of the cruciferous type. Stomata generally present on both surfaces in the Illecebraceae of Bentham and Hooker, as well as in *Honckenya peploides* (L.) Ehrh. (Syn. *Arenaria peploides* Linn.) (Warming 2362), certain *Cerastium* spp., *Colobanthus quitensis* Bartl. (Betts 187) (most numerous on the upper side), *Polycarpaea corymbosa* (L.) Lam. (Sabnis 1977), *Saponaria officinalis* Linn. (Holm 1057). Groups of stomata, overlying patches of pale-coloured parenchyma situated at the ends of veins, occur in the teeth of young leaves of the genera included by Bentham and Hooker in the Caryophylleae. Stomata in certain narrow-leaved arctic species have the pores parallel to the longitudinal axis of the leaf. **Hypoderm** recorded towards the lower surface in a species of *Colobanthus*, and a collenchymatous pseudo-hypoderm in *Saponaria* (Simmler 2100). **Mesophyll** centric or dorsiventral, vascular strands surrounded by water-storage cells in species with centric leaves. Dorsiventral, with palisade tissue towards the upper (adaxial) surface in *Colobanthus quitensis* Bartl. (Betts 187), an arctic species of *Minuartia* (Warming 2362), *Saponaria officinalis* Linn. (Holm 1057), but, according to Simmler (2100) palisade tissue sometimes occurs towards both surfaces in this genus or alternatively the whole of the mesophyll is composed of rounded cells, those towards the centre of the leaf being slightly larger. A normal dorsiventral mesophyll also recorded in certain species of *Siphonochia*. Dorsiventral mesophyll with palisade tissue towards the abaxial surface in a few species of *Cerastium*, *Melandrium*, *Minuartia*, *Silene*, and *Viscaria* recorded by Warming (2362). Distribution of palisade tissue variable in certain arctic species, notably of *Cerastium* and *Minuartia*. Lacunae observed, also by Warming, in the spongy mesophyll towards the adaxial surface in a few species of *Cerastium*, *Melandrium*, *Silene*, and *Viscaria*. Stellate cells recorded in the spongy mesophyll of *Cerastium* sp. Centric mesophyll mentioned by various authors in *Achyronychia* and in certain species of *Arenaria*, *Cardionema*, *Cometes*, *Corrigiola*, *Dicheranthus*, *Dysphania*, *Gymnocarpus*, *Habrosia*, *Haya*, *Hernieria*, *Illecebrum*, *Paronychia*, *Pollichia*, *Polycarpaea*, *Pteranthus*, *Scleranthus*, *Sclerocephalus*, *Siphonochia*. **Midrib**, in transverse sections, exhibiting one main vascular bundle accompanied by two smaller ones in *Scleranthus biflorus* (Forst.) Hook. according to Foweraker (703). One bundle enters the leaf in certain arctic species, but divides to form three in species with narrow leaves, or a greater number in those with broader ones (Warming 2362). Vascular bundles not usually accompanied by sclerenchyma except in certain

species of *Arenaria*, *Cardionema*, *Habrosia*, *Melandrium*, *Minuartia*, *Pollichia*, *Scleranthus*, and *Silene*. Calcium oxalate commonly present in the form of large, conspicuous cluster **crystals** in many genera and species including *Arenaria*, *Corrigiola*, *Gymnocarpus*, *Minuartia* sp., *Pteranthus*, *Scleranthus*, *Silene*. The abundance of the crystals sometimes varies within a single species in specimens from different localities. Crystal-sand also recorded in *Dysphania*, *Gymnocarpus*, *Habrosia*, and other genera. **Tanniniferous substances** present in *Polycarpaea corymbosa* Lam. according to Sabnis (1977).

AXIS

STEM (Fig. 38 E and G)

Epidermis including longitudinal rows of papillose cells in *Loeflingia*, *Ortegaia*, *Polycarpon*, and *Stipulicida*. **Cork** usually arising in the pericycle, e.g. in certain species of *Dianthus*, *Honckenya*, *Lychnis*, *Polycarpaea*, *Sagina*, *Saponaria*, *Silene*, *Stellaria*; arising in the outermost part of the cortex in *Spergularia*; sub-epidermal in *Paronychia*. **Cortex** not usually exhibiting distinctive features, frequently narrow and sometimes containing assimilatory tissue (*Dianthus*, &c.); the inner part consisting of small cells with very thick mucilaginous walls, e.g. in a species of *Colobanthus*, but with an outer zone of small suberized cells between this and the epidermis (Betts 187); consisting of thick-walled cells, giving a dark-brown colour when treated with chlorzinciodide, in *Scleranthus biflorus* (Forst.) Hook. (Foweraker 703); completely sclerenchymatous in *Drypis spinosa* Linn. (Friedel and Yen 719). **Endodermis** frequently well defined, e.g. in certain species of *Arenaria*, *Corrigiola*, *Dianthus*, *Lychnis*, and *Saponaria*. **Pericycle** characterized by a sclerenchymatous ring of varying width in different genera and species. With a broad ring up to about 10 cells wide in certain species of *Dianthus*, *Lychnis*, *Minuartia*, and *Silene*; with a ring 4–6 cells wide in certain species of *Cometes*, *Corrigiola*, *Gymnocarpus*, *Herniaria*, *Illecebrum*, *Lychnis*, *Paronychia*, *Pollichia*, *Pteranthus*, *Saponaria* (not in very young stems), *Scleranthus*, and *Silene*; with a ring 1–2 cells wide in *Herniaria* sp. Pericycle described by Friedel and Yen (719) as wholly sclerenchymatous in *Drypis*. Outer part of the sclerenchymatous ring more strongly lignified and composed of cells with narrower lumina than the part towards the phloem, the prosenchymatous nature of the inner elements being visible only in longitudinal sections, in certain species of *Gypsophila*, *Lychnis*, *Saponaria*, and *Silene*. Ring of fibres accompanied by groups of stone cells in *Polycarpaea corymbosa* (L.) Lam. according to Sabnis (1977). The pericyclic sclerenchyma becomes split up into separate strands in species with a considerable amount of secondary thickening. **Vascular bundles** individually distinct in transverse sections, but tending to become united to form relatively large arcs in certain species of *Arenaria*, *Corrigiola*, *Drypis*, *Lychnis* (Fig. 38 G), *Paronychia*, *Polycarpaea*, *Saponaria* (rarely in this genus), *Scleranthus*, *Silene*, *Spergula*, *Stellaria*. Bundles not individually distinct, but xylem and phloem forming continuous rings in certain species of *Dianthus*, *Gymnocarpus*, *Gypsophila* (Fig. 38 E), *Herniaria*, *Minuartia*, *Paronychia*, *Pollichia*, *Sagina*, *Saponaria* (most species), *Silene*, *Spergularia*. Phloem forming a continuous ring, but accompanied by xylem in separate strands in certain species of *Arenaria*, *Buffonia*, and *Telephium*. Vessels with simple perforations. A large proportion of the phloem often consists of

parenchyma. For **anomalous thickening** see below. Calcium oxalate, in the form of large cluster **crystals** occurs in certain species of *Dianthus*, *Herniaria*, *Lychnis* (chiefly in the endodermis), *Saponaria* (not in the endodermis), *Silene* (in the endodermis). Solitary crystals rare, said to be confined to *Polycarpaea*.

WOOD

Vessels with simple perforations. **Parenchyma** frequently constituting a large proportion of the wood. **Rays** generally absent, except for the tissue between the bundles in those species in which they are individually distinct. **Fibres** with simple or bordered pits. The anatomy of the woody '*Dianthus arboreus*' (syn. *D. aciphyllus* Sieb.) has been fully described by Tellini (2240).

ROOT

Structure best known in *Saponaria officinalis* Linn. which is described under 'Economic Uses'. Roots of *Silene vulgaris* Linn. grown in different kinds of soil were found by Millner (1538) to differ in the amount of periderm formed, and to have more numerous vessels when grown in sand than in clay. Minor differences between the root structure of closely related species of *Silene* also recorded by the same author.

ANOMALOUS SECONDARY THICKENING

Concentric rings of xylem and phloem or of individually distinct vascular bundles occur in the roots and/or sometimes the old stems of certain species of *Acanthonychia*, *Achyronychia*, *Cardionema*, *Cerdia*, *Cometes*, *Corrigiola*, *Dysphania*, *Haya*, *Leptogonium*, *Ortega*, *Pollichia*, *Polycarpaea*, *Polycarpon* (Fig. 37 D), *Pycnophyllum*, *Silene*, *Spergula*, *Spergularia*, *Stipulicida*, *Telephium*, and possibly other genera. For further details see Pfeiffer (1712). Although secondary thickening is usually normal in *Acanthophyllum*, the broad rings of secondary xylem are interspersed with narrow bands of unligified parenchyma in certain species. In other species the initial ring of normal bundles becomes split up into 4 isolated strands of xylem and phloem by radial groups of parenchyma. Later on 4 meristematic areas arise in the pith opposite the xylem strands and give rise to inversely orientated xylem and phloem which eventually unite with the outer vascular tissues.

TAXONOMIC NOTES

The anatomical characters of the genera included by Bentham and Hooker in the family Illecebraceae are so similar to those of the Caryophyllaceae that both groups have been described together as in the system of Engler and Prantl. It is not possible from the anatomical facts which are at present available to decide to which of the tribes of the Caryophyllaceae the Illecebraceae may belong, because the existing tribes of the first of these groups do not themselves seem to be very well defined on anatomical grounds. Further research may enable this matter to be cleared up.

Another family whose floral characters resemble those of the Caryophyllaceae is the Polygonaceae. The anatomical feature which seems to lend most support to this relationship is the occasional occurrence of anomalous secondary thickening in both families. It is also interesting to note that the

dominant form in which calcium oxalate is secreted in both families is the cluster crystal. Other anatomical features of the two families are not sufficiently distinctive to provide conclusive evidence of their close relationship, although there are no known facts which make their close connexion seem improbable.

The position in the Centrospermae in which the Caryophyllaceae (including Illecebraceae) have been placed in the Engler system differs considerably from the position to which the family is assigned in the Genera Plantarum of Bentham and Hooker. One of the most outstanding features of the Centrospermae is the widespread occurrence of anomalous secondary thickening throughout the group. On these grounds there seems to be good reason for including the Caryophyllaceae in the order since anomalies of the same kind occur sporadically in the family. The widespread occurrence of crystal-sand and cluster crystals in the Amaranthaceae brings this family more into line with the Caryophyllaceae than some of the other families in the Centrospermae such as the Phytolaccaceae where raphides predominate. Evidence of affinities between the Caryophyllaceae and Portulacaceae is afforded by the occurrence of saponin in certain members of both families. On the other hand, the occurrence of interxylary phloem in the Portulacaceae tends rather to demarcate this family from the remainder of the Centrospermae with the exception of the Basellaceae.

ECONOMIC USES

The family contains many well-known ornamental garden plants such as Carnations, Pinks, Gypsophilas, &c. The Soap Root obtained from *Saponaria officinalis* Linn. contains saponin, and has in the past been used for medicinal purposes. Its anatomical characters include the following. Root covered externally by a layer of brown cork cells. Secondary phloem consisting of sieve tubes and parenchyma. Xylem composed mainly of parenchyma, but including scattered vessels, which are solitary or tending to be in radial rows. Rays absent. Calcium oxalate, mostly in the form of conspicuous cluster crystals but also occurring as crystal-sand, secreted in all parenchymatous tissues. Starch absent. Saponin present. Structure somewhat similar in *Silene*, but vessels in the older roots becoming twisted.

The root of *Corrigiola littoralis* Linn. has sometimes been substituted for that of *Anacyclus pyrethrum* (Family Compositae, see p. 802) which is used in medicine. Transverse sections of the root of *Corrigiola littoralis* exhibit a central xylem mass which tends to be radially dissected, surrounded by concentric rings of vascular bundles.

GENERA DESCRIBED

Achyronichia, Arenaria,* Buffonia, Cardionema, Cerastium, Cerdia, Colobanthus, Cometes, Corrigiola,* Dianthus,* Dicheranthus, Drypis, Dysphania, Gymnocarpus, Gypsophila,* Habrosia, Haya, Herniaria,* Honckenya, Illecebrum, Loefflingia, Lychnis,* Melandrium, Minuartia,* Ortega, Paronychia, Pollichia, Polycarpaea, Polycarpon, Pteranthus, Pycnophyllum, Sagina, Saponaria,* Scleranthus,* Sclerocephalus, Silene,* Siphonichia, Spargula, Spargularia, Stellaria,* Stipulicida,* Telephium, Viscaria.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Betts 187, Bonnet 230, Chkhubianishvili 397, Correns 476, Foweraker 703, Friedel and Yen 719, Holm 1057, Joshi 1197, Millner 1538, Pax and Hoffmann 1677, Pfeiffer 1712, Privault 1759, Sabnis 1977, Simmler 2100, Starr 2188, Tellini 2240, Warming 2362.

43. PORTULACACEAE

(FIG. 36 on p. 154; FIG. 38 on p. 160)

SUMMARY

Herbs, or small shrubs, often succulent, and frequently containing abundant mucilage in the parenchyma cells of the leaf and stem. The family is widely distributed but occurs chiefly in the New World. The presence of mucilage and the comparatively poor development of mechanical tissue make it very difficult to cut freehand sections of members of this family. The **hairs** may be (i) simple, unicellular in *Calandrinia*; (ii) in the form of papillae, e.g. in *Spraguea*, and *Talinum*; (iii) multicellular and shaggy, the superficial cells sometimes being papillose (Fig. 36 c); (iv) branched in *Calandrinopsis*; (v) uniseriate and glandular (Fig. 36 d). The **stomata** are somewhat variable, but sometimes rubiaceous with 2 or 4 subsidiary cells parallel to the pore. **Crystals** of calcium oxalate occur in the form of (i) clusters; (ii) solitary prisms; (iii) crystal-sand consisting of acicular crystals. The structure of the **mesophyll** is very variable and exhibits several interesting types of structure probably to be regarded as ecological specializations (see 'Leaf'). The fleshy leaves of *Portulaca grandiflora* Hook. are provided with a shallow groove in the adaxial surface. The **pericycle** of the stem includes a sclerenchymatous ring in some species, but in many others mechanical elements are lacking in this region. The **vascular bundles** of the axis appear separate and individually distinct in transverse sections of most species, although exceptions occur. In the xylem the vessels are provided with simple perforations, and the fibres of the ground tissue with simple pits.

LEAF

Cuticle thick in *Ceraria namaquensis* Pearson et Stephens but thin in *Portulacaria afra* Jacq., according to Michell (1511). **Hairs** as described in the 'Summary' above; said to be absent from the Montioideae with the exception of *Wangerinia*. **Epidermis** including solitary cells with the form of bladder-like protrusions from the surface in *Spraguea* and *Talinum*. **Hypoderm** of thick-walled, unligified cells recorded beneath the lower epidermis in *Lenzia*. **Stomata** (Fig. 36 B) present on both surfaces of the leaf in most instances; confined to the lower surface in *Montia australasica* (Hook. f.) Pax et Hoffmann (syn. *Claytonia australasica* Hook. f.) according to Betts (187); most numerous on the lower surface in certain species of *Portulaca*, *Spraguea*, and *Talinum*; rubiaceous, accompanied by 4 subsidiary cells parallel to the pore in *Calandrinia* or by 2 in some of the other genera and species. True subsidiary cells absent from *Montia*. **Mesophyll** of the succulent leaves varying greatly in structure. (i) Dorsiventral, e.g. in *Montia australasica* according to Betts (187). (ii) Consisting of assimilatory and

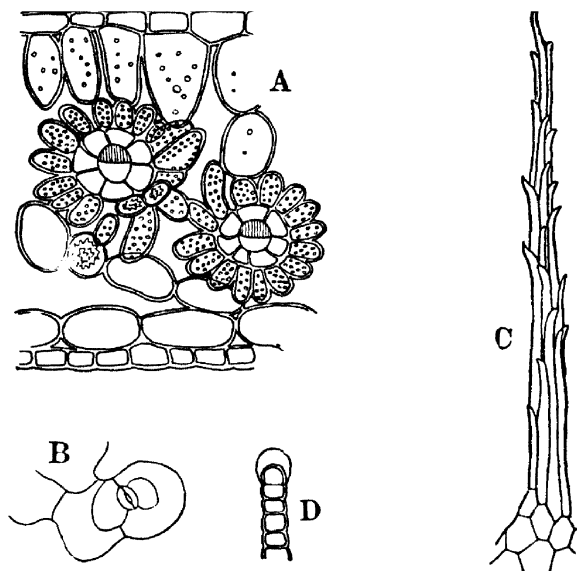


FIG. 36. *PORTULACACEAE*

A, Transverse section of the leaf of *Portulaca oleracea* Linn. B, Stomatal apparatus of *Portulaca oleracea*. C, Shaggy hair, and D, Glandular hair of *Calandrinia umbellata* DC.—After Vesque.

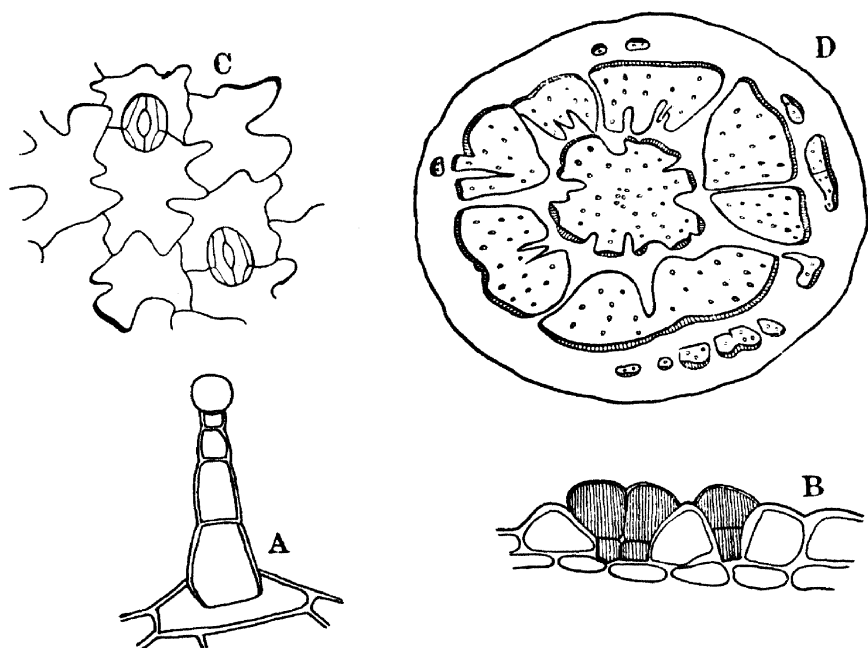


FIG. 37. *CARYOPHYLLACEAE*

A, Glandular hair of *Silene villosa*, Forsk. B, Transverse section through the outermost part of the sticky region of the stem of *Viscaria viscosa* (Scop.) Aschers. C, Epidermis of the leaf with stomata in *Viscaria viscosa*. D, Transverse section through the root of *Polycarphaa fragilis*, Delile.—By Solereder.

large water-storage cells either intermingled or localized in separate zones. Assimilatory cells forming a network between the water-storage cells in *Portulaca hirsutissima* Cambess; confined to the sub-epidermal region on either side of the leaf, the centre being occupied by water-storage cells in *Portulaca tuberosa* Roxb. (iii) Consisting almost wholly of water-storage cells, the vascular bundles alone being surrounded by green palisade cells in certain species of *Portulaca* (Fig. 36 A).

Vascular bundles in the **veins** not accompanied by sclerenchyma; but sometimes surrounded by a sheath of large, colourless, parenchymatous cells, e.g. in *Portulaca grandiflora* Hook. and *P. oleracea* Linn. (Fig. 36 A). **Petiole**, in transverse sections through the distal end, exhibiting a solitary vascular strand in *Portulaca grandiflora* and *P. oleracea*, the strand being surrounded by a well-defined endodermis in the last named species. **Crystals** exclusively clustered in *Calyptridium*, *Lewisia*, *Monocosmia*, *Portulaca*, *Portulacaria*, and *Talinum*; occurring as mixed solitary and clustered forms in *Anacampseros*, *Calandrinia*, *Spraguea*; crystal-sand, consisting of small needles and prisms recorded in *Calandrinia*. No crystals observed in *Montia*. **Mucilage cells** generally present, sometimes especially large in *Anacampseros* and *Portulacaria*.

AXIS

STEM (Fig. 38 A and C)

Epidermis composed of dome-shaped cells with thick cuticle in *Montia australasica* (Hook. f.) Pax et Hoffmann (syn. *Claytonia australasica* Hook. f.) according to Betts (187), and, of polygonal cells in certain species of *Portulaca* according to Sabnis (1977). Bodies, believed to be composed of an organic substance, recorded by Kisser (1239) as being included within the walls between the epidermal cells, and in those between the epidermis and adjacent collenchyma in '*Portulaca gilliesii*'. Similar bodies apparently absent from herbarium specimens of other members of the genus or in other genera of the family examined at the same time. **Cortex** broad, consisting of large, thick-walled cells with intercellular spaces between them in *Montia australasica*. Outer part of the cortex consisting of thin-walled parenchyma filled with starch, but the inner part containing chlorophyll in certain species of *Portulaca*. Sclerenchymatous cells recorded by Michell (1511) in the cortex, opposite the vascular bundles of species of *Ceraria*. **Endodermis** well defined in *Montia australasica*; not conspicuous in species of *Ceraria*. **Pericycle** frequently without sclerenchyma, e.g. in certain species of *Montia* and *Portulaca*, but including mechanical elements in some of the Portulacoideae, e.g. in *Calandrinia caulescens* H. B. et K. A continuous ring of sclerenchyma noted in the pericycle of *Lenzia*. **Vascular bundles** collateral, appearing individually distinct and arranged in a ring in transverse sections of the species of *Calandrinia*, *Montia*, and *Portulaca* available for examination; also recorded as being separate in *Ceraria* and *Lenzia*. Bundles deeply seated and stated by Sabnis (1977) to be separated by uniseriate rays in certain species of *Portulaca*. Xylem and phloem recorded by Betts (187) as being in the form of a continuous cylinder in *Montia australasica*. Phloem accompanied towards the outside by considerable masses of fibres in species of *Ceraria*. Xylem containing tangential bands of parenchyma in *Portulacaria afra* Jacq. Vessels small, with simple perforations; sometimes tending to be in radial rows; with

simple pits in *Ceraria gariepina* Pears. et Steph., according to Michell (1511); with spiral thickening in *Montia perfoliata* (Don.) How, *Portulaca grandiflora* Hook., *P. oleracea* Linn., and probably in other species as well. **Intraxylary phloem** stated by Pax and Hoffmann (1676) to occur in *Montia* and its allies, but observations at Kew show that it is not always well defined. **Pith** varying in size in different species, generally consisting of thin-walled cells. Dark-brown **mucilage cells** commonly present according to Michell (1511), those in two species of *Ceraria* being in the form of a ring, or forming a network amongst water-storage cells in the cortex. Drops of fixed **oil** present throughout the stem in certain species of *Ceraria*, according to the same author.

BARK

Leathery, easily detached from the stem, and sometimes containing an inflammable material in species of *Ceraria*; thinner, but similar in structure in species of *Portulacaria* according to Michell (1511).

TAXONOMIC NOTES

The anatomical characters of the Portulacaceae as a whole are not sufficiently distinctive to provide reliable evidence concerning the affinities of the family. There seems no definite reason for not accepting the commonly held view that the Portulacaceae and Caryophyllaceae are near relatives, both included in the Centrospermae. The occurrence of saponin in certain of the Portulacaceae as well as in some of the Caryophyllaceae provides additional evidence of the close relationships between the two families.

An attempt has been made by Chorinsky (408), who compared the epidermal outgrowths of *Anacampseros* with those of *Pereskia* and *Rhipsalis*, to establish the existence of affinities between the Portulacaceae and Cactaceae. The evidence afforded by this comparison is stated to indicate the existence of affinities between these two families, but this fact, taken by itself, does not appear to be very convincing.

ECONOMIC USES

Certain members of this family are commonly cultivated in English gardens, but they are not of any economic importance. Species of *Montia*, *Portulaca*, and *Talinum* have sometimes been used as pot-herbs, while *Lewisia rediviva* Pursh is also edible.

GENERA DESCRIBED

Anacampseros, *Calandrinia*,* *Calandriniopsis*, *Calyptridium*, *Ceraria*, *Hectorella*, *Lenzia*, *Lewisia*, *Monocosmia*, *Montia*,* *Portulaca*,* *Portulacaria*, *Spraguea*, *Talinum*, *Wangerinia*.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Betts 187, Chorinsky 408, Kisser 1239, Marroquin and Howard 1446, Michell 1511, Pax and Hoffmann 1676, Sabnis 1977.

44. TAMARICACEAE

(FIG. 34 on p. 144; FIG. 38 on p. 160)

SUMMARY

(i) GENERAL

Shrubs or trees with slender branches and small needle-like or scale leaves, which grow chiefly on desert or saline soils in the Mediterranean region and Central Asia. The **leaf** is generally centric, the centre of the mesophyll being composed of water-storage cells, whilst the mostly ranunculaceous **stomata** are usually present on both surfaces or confined to the upper side. The pores of the stomata are usually arranged transversely to the course of the veins. **External glands** which secrete mineral salts have been recorded on the leaves of all genera and on the stem of certain species of *Tamarix*. According to Brunswick (296) the solitary or clustered **crystals** which are generally present consist of gypsum and not of calcium oxalate.

(ii) WOOD

Vessels small to medium-sized; solitary, in short multiples and in clusters; semi-ring-porous, perforations simple, intervacular pitting alternate and very small, pits to parenchyma similar, members extremely short. **Parenchyma** scanty paratracheal to vasicentric, storied, fusiform cells common. **Rays** very wide (up to 25 cells wide) and very high, heterogeneous. **Fibres** with simple pits, moderately to extremely short.

LEAF

Cuticle smooth, fairly thick, striate or punctate. **Hairs** scanty, where present unicellular with thick walls and narrow lumina. **External glands** (see 'Summary') frequently embedded in the mesophyll. **Epidermis** composed of cells with straight anticlinal walls; papillose in a few species of *Myricaria*, *Reaumuria*, and *Tamarix*. **Stomata** present on both surfaces or confined to the upper side, with the pore placed transversely to the course of the veins in *Hololachne*, *Myricaria*, *Reaumuria*, and *Tamarix*, but exceptions recorded in *Reaumuria*; generally ranunculaceous, but said to be rubiaceous in a species of *Myricaria*. **Mesophyll** centric except in certain species of *Tamarix* with an abortive lamina, palisade tissue in the latter being confined to the lower surface of the leaf sheath which is directed towards the light. Branched fibres, present in the mesophyll of *Reaumuria oxiana* Boiss., extend between the elongated palisade cells to the epidermis. Storage-tracheids, sometimes extending to the epidermis, also recorded in certain species of *Reaumuria* and *Tamarix*. Vascular bundles of the **veins** not usually accompanied by sclerenchyma, except sometimes in *Tamarix*; embedded in the mesophyll. Solitary and cluster **crystals** very common; said by Brunswick (296) to consist of gypsum and not of calcium oxalate; generally present in the mesophyll or beside the vascular bundles in *Hololachne*, *Myricaria*, and *Tamarix*. **Tannin** often present in the palisade tissue.

AXIS

YOUNG STEM (Fig. 38 D)

External glands, similar to those on the leaf, recorded by Sabnis (1977) in certain species of *Tamarix*. **Cork** superficial and durable in *Tamarix*;

formed from a succession of phellogens and easily detached in *Reaumuria* according to Brunner (295). **Cortex** generally consisting of large or small, thin-walled parenchymatous cells, the outer part composed of assimilatory cells in certain species. Cortex also including water-storage tracheids with pitted or scalariform thickenings, and isolated, enlarged, stone cells in certain species of *Tamarix*. **Pericycle** containing strands of fibres, which form a continuous ring in young stems but become more widely separated by parenchyma when older. **Phloem** present in the form of a continuous ring or in strands. Secondary phloem usually containing massive strands of fibres, which are convex towards the exterior and arranged in tangential series as seen in transverse sections. Phloem fibres lacking in *Reaumuria*. **Xylem** constituting a large proportion of the total diameter of the stem even when young, being present in the form of a cylinder traversed by the fairly broad primary rays in *Tamarix* (Fig. 38 D). Vessels with simple perforations. **Pith** consisting of thick-walled cells in species of *Tamarix*. **Crystals**, stated by Brunswick (296) to consist of gypsum, present in the pith and cortex of *Hololachne*, *Myricaria*, and *Tamarix*. **Tannin** often abundant.

WOOD (Fig. 34 H-I)

Vessels medium-sized (mean tangential diameter usually 100–20 μ) in most species of *Tamarix*, small (less than 100 μ) in *Myricaria* and *Tamarix* p.p.; solitary, in short multiples and in clusters; 3–12 per sq. mm.; semi-ring-porous in some species of *Tamarix* and ring-porous in *Myricaria* (185). Perforations simple, transverse. Intervascular pitting alternate, very small to minute; pits to ray cells similar. Mean member length 0.1–0.2 mm. **Parenchyma** paratracheal, as a few cells to broad sheaths round the vessels and vessel groups (Fig. 34 H). Strands of 1–2 cells; fusiform cells common. Storied. **Rays** up to 25 cells wide in *Tamarix articulata* Vahl., but usually up to 10–15 cells wide in other species; often up to 2 mm. high; uniseriatae rare or absent; rays very few, commonly not more than 2 or 3 per mm.; heterogeneous, the rays often appearing as homogeneous in tangential sections (Fig. 34 I), but with several rows of square cells on the margins and sheathing the rays. Numerous solitary crystals sometimes present, e.g. in *T. tetragyna* Ehrb.; Brown (1679) reports occasional druses in *T. articulata*. **Fibres** with few, simple pits, almost entirely limited to the radial walls. Walls moderately thin. Mean length 0.4–0.9 mm.

TAXONOMIC NOTES

The occurrence of similar external glands in the Frankeniaceae and Tamaricaceae is taxonomically interesting, but it is important to realize that the glands are probably ecological specializations which may have arisen independently in the two families. See also under 'Frankeniaceae'.

ECONOMIC USES

Tamarix galls are used in India in native medicines, as well as for dyeing or tanning. They are occasionally used as a substitute for oak galls. Tamarix manna, which is obtained from twigs punctured by insects, is also used for medicinal purposes in India. The wood is of no commercial importance. It was commonly used for dowels by the Ancient Egyptians.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Hololachne, Myricaria, Reaumuria, Tamarix,* (Fouquiera is described under Fouquieraceae).

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Myricaria), Tamarix.

LITERATURE

(i) *On General Anatomy*

Brunner 295, Brunswick 296, Niedenzu 1597, Sabnis 1977, Zemke 2505.

(ii) *On Wood Structure*

Chowdhury 411, Dadswell and Record 533, Greguss 2522, Howard 1088, Messeri 1493, Pearson and Brown 1679, Record 1843, 1851, Trabut 2274.

45. FOUQUIERACEAE

(FIG. 34 on p. 144; FIG. 38 on p. 160)

SUMMARY

(i) GENERAL

A small family of peculiar dwarf shrubs or small trees confined to south-western North America, consisting of the two genera *Fouquiera* and *Idria*. *Fouquiera* includes several species of shrubs or small trees, 15–20 ft. high, with numerous branches radiating from a short, often inconspicuous trunk. *Idria*, of which only one species is known, is a stem succulent with a greatly swollen trunk somewhat resembling an inverted parsnip, bearing fleshy branches and spines, and sometimes attaining a height of 40 ft. when mature. Young plants somewhat resemble kohlrabi. The anatomical structure of the two genera differs somewhat in correlation with their divergence in habit, so they are here described separately.

(ii) WOOD

Vessels small, with a slight tangential or radial pattern, often ring-porous, with simple perforations, members moderately short. **Parenchyma** diffuse. **Rays** 4–6 cells wide, often composed almost entirely of square to upright cells. **Fibres** with small bordered pits, of medium length.

FOUQUIERA

LEAF

Not definitely dorsiventral. **Spines** arising as described below for *Idria*. **Epidermis** sometimes including cells with mucilaginous inner walls. **Stomata** present on both surfaces; ranunculaceous.

AXIS

STEM (Fig. 38 F and H)

Very striking in general appearance owing to the reticulate pattern of corky layers on the surface. Young stems furrowed and provided with a narrow

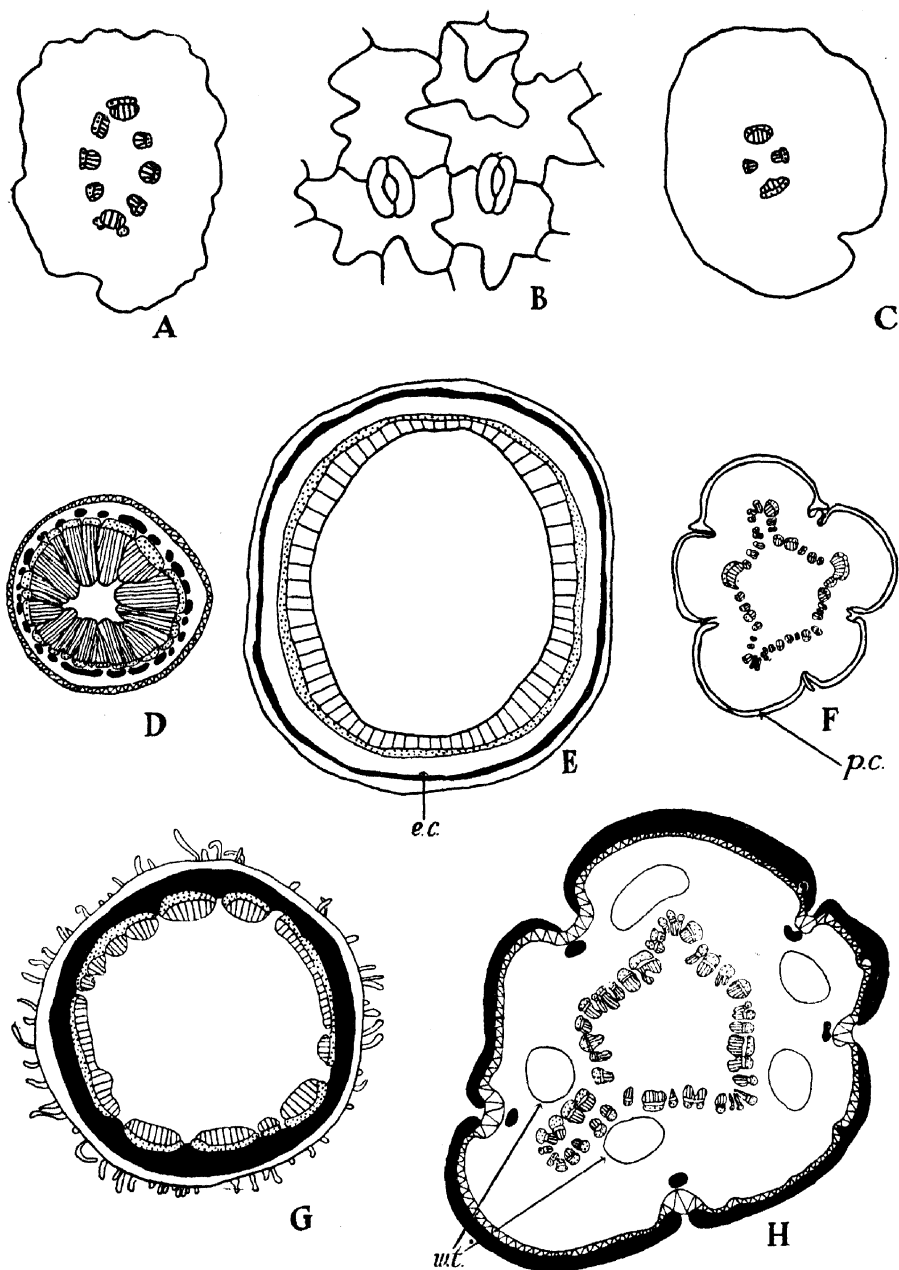


FIG. 38. *PORTULACACEAE*, A and C; *CARYOPHYLLACEAE*, B, E, and G; *TAMARICACEAE*, D; *FOUQUIERACEAE*, F and H

A, *Portulaca oleracea* Linn. Stem $\times 23$. B, *Saponaria officinalis* Linn. Stomata $\times 250$. C, *Montia perfoliata* (Don.) How. Stem $\times 23$. D, *Tamarix gallica* Linn. Stem $\times 13$. E, *Gypsophila paniculata* Linn. Stem $\times 8$. F, *Fougiera splendens* Engelm. Young stem $\times 10$. G, *Lychnis coronaria* Des. Stem $\times 10$. H, *Fougiera splendens* Engelm. Stem $\times 10$.

Fig. B, stomata on lower surface of leaf. F, Showing furrows and ring of close vascular strands. e.c. Slightly elongated cells with thickened walls. p.c. Layer of small somewhat prosenchymatous cells. w.t. Water-storage cells.

layer of fibres with thick walls and narrow lumina immediately within the epidermis except at the bases of the furrows. The fibrous layer, which is described by Solereder as cork, becomes wider with increase in age owing to secondary division of cells in the sub-epidermal region. **Cork**, consisting of cells with thin walls and wide lumina, is subsequently formed internally to the fibres, the stem eventually becoming covered with bark consisting of paper-like layers capable of burning with a smoky flame owing to the presence of waxy material. Primary **cortex**, according to Scott (2069) consisting mainly of parenchyma, but stated to contain assimilatory tissue of varying width; also including collenchyma and groups of stone cells. A continuous network of water-storage cells throughout the cortex is particularly evident in sections mounted in chlor-zinc-iodide because the component cells remain unstained in contrast to the adjacent starch-filled parenchyma. **Vascular bundles** separated by wide primary rays in young stems. **Phloem** appearing in transverse sections as irregular, triangular wedges; including sieve tubes with lateral sieve plates. **Xylem** exhibiting seasonal growth rings. **Pith** stated by Scott (2069) to be horizontally septate. Abundant **crystals**, believed to consist of silicates, recorded by Reiche (1908).

WOOD (Fig. 34 J-K)

Vessels very small (25-50 μ mean tangential diameter) or slightly larger; solitary and in clusters (Fig. 34 K), and often with a tangential pattern or irregular radial rows or groups (1886); about 60 per sq. mm.; semi-ring-porous to distinctly ring-porous. Perforations typically simple, but Solereder refers to occasional scalariform plates with few bars. Intervascular pitting often elongated horizontally, varying from round and alternate to almost scalariform in the smaller vessels; some pits to ray cells similar to the intervascular pitting, others larger and simple or with only narrow borders. Mean member length 0.3 mm. (100). **Parenchyma** apotracheal, as numerous scattered cells and short, uniseriate lines. Strands of 2-4 cells. **Rays** up to 6 (occasionally 8) cells wide; often up to about 1 mm. high; uniseriate rather few; about 5 rays per mm.; uniseriate and multiseriate rays often composed almost entirely of square to upright cells (Fig. 34 J). **Fibres** with small bordered pits, mostly on the radial walls; walls thick and mostly gelatinous; mean length 1.1 mm. (96).

ROOT

Bounded externally by laminated **cork**. **Water-storage cells** not seen by Scott (2069) in the disintegrating cortex of old roots.

(The respective accounts of the anatomy of *Fouquieria* given by Reiche (1908) and Scott (2069) differ in certain details.)

IDRIA

The following description is based mainly on Humphrey's (1110) account.

LEAF

Leaves of wild specimens with palisade tissue on both sides and 2-4 layers of spongy tissue at the centre. Palisade tissue sometimes confined to the upper surface in greenhouse material. **Stomata** flush with the surface of the

lamina. **Veins** embedded in the central spongy tissue. **Petiole** of a nearly mature leaf containing a fairly thick, semicircular vascular strand, concave upward as seen in transverse section. **Spines**, when first formed, attached to the abaxial side of the lamina and extending down the branches for a short distance; becoming separated from the lamina and petiole at the time of leaf fall by an abscission layer, a small scar remaining to indicate where the vascular strand passed from the cortex into the petiole.

AXIS

MAIN TRUNK

Exterior bounded by **cork** consisting of many rows of yellowish, compressed cells. Outer part of the **cortex** containing large groups of stone cells, the latter forming an almost continuous ring round the stem; inner part parenchymatous, with simple pits between the cells giving the appearance of a perforated Swiss cheese. Cortex also including water-storage cells. **Phloem** appearing in transverse sections as slender or wedge-shaped groups, most of the tissues becoming crushed, apparently owing to pressure against the sclerenchymatous sheath in the cortex. Outer part of the **xylem** consisting of a narrow, almost continuous cylinder, broken by narrow bands of radial parenchyma extending into the phloem. Inner part of the xylem mainly parenchymatous, containing numerous lacunae. Scattered vessels present in the parenchyma in roughly concentric rows; probably pushed into these positions by proliferation of the intervening parenchymatous cells. Vessels of the secondary xylem with circular or slit-like pits in the radial and tangential walls. **Pith** consisting of homogeneous parenchyma, the cells tending to be vertically elongated.

BRANCH

The following regions recognizable in a typical branch 6.6 mm. in diameter. (i) **Cork** in the form of a thick layer. (ii) **Cortex** half as wide as the cork. (iii) A narrow **phloem**. (iv) **Xylem**, about as wide as the cork; not divided into tracheal and parenchymatous portions as in the main stem, and consisting of vessels, fibres, and parenchyma. Wood fibres with numerous small pits; many of them septate. Vessels up to $38\ \mu$ in diameter; minimum length of the component members $280\ \mu$; pits in the lateral walls circular to slit-shaped. **Pith** with radius about equal to that of the xylem, composed of rather thick-walled parenchymatous cells with simple pits.

TAXONOMIC NOTES

There has been considerable disagreement concerning the taxonomic position of the family. *Fouquiera*, in the Bentham and Hooker system, is treated as a member of the Tamaricaceae, whilst in the Engler system *Fouquiera* and *Idria* have been placed in a separate family close to the Tamaricaceae. Reiche (1908), after reviewing the various taxonomic positions which have been proposed for the family, could do no more than conclude that it is a primitive member of the Sympetalae. Humphrey (1110) has also reminded us that possible affinities with the Loasaceae and Polemoniaceae have also been suggested.

The wood structure of *Fouquiera* indicates that there is no good reason for

putting this genus in the same family as *Tamarix*. *Tamarix* has highly specialized wood with short elements, stories, libriform fibres, and paratracheal parenchyma; *Fouquieria* is at a relatively low level of specialization, with fibre tracheids, &c. and apotracheal parenchyma. Hutchinson (1113) includes the Fouquieraceae and the Malesherbiaceae in the Tamaricales.

GENERA DESCRIBED

Fouquieria,* Idria.

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Humphrey 1110, Hutchinson 1113, Reiche 1908, Scott, F. M. 2069.

(ii) *On Wood Structure*

Record 1843, 1851, Record and Hess 1886.

46. ELATINACEAE

SUMMARY

A small, cosmopolitan family of herbs or shrublets, often aquatic, included in the 2 genera *Bergia* and *Elatine*. A **secretion**, brownish when dry, and probably resinous in nature, is widely distributed in the tissues, or deposited in a granular form on the surface of the stem.

LEAF

Hairs entirely absent from *Elatine* and 10 species of *Bergia* examined by Pottier (1735). Other species of *Bergia* are provided with uni- or bicellular, and less frequently with uniseriate trichomes. Glandular hairs, consisting of a multicellular short column bearing a rounded head, also occur in *Bergia*. Six species examined by Pottier possessed only glandular hairs, but others had mixtures in various proportions of glandular and non-glandular hairs. Whole surface of the plant covered with conical hairs consisting of 1 to several cells in *Bergia arenarioides* (Camb.) Fenzl. and *Bergia suffruticosa* (Delile) Fenzl. according to Niedenzu (1595). **Epidermis** consisting of cells with sinuous anticlinal walls, those on the upper generally less undulating than those on the lower side, but varying considerably in this respect in different species of *Bergia*. Epidermal cells often very variable in size, especially in *Bergia*, the larger ones serving for water storage, and sometimes appearing as glistening spots on the surface when viewed with a lens. Particularly large cells, deeply stained by alum carmine, present in the epidermis of *Elatine californica* Gray. **Stomata** present on both surfaces, variable in size, appearing at first sight to be ranunculaceous, but careful examination shows them nearly always to be accompanied by 2 cells parallel to the pore and with 2 more at right angles to them. **Mesophyll** of *Bergia* spp. composed mainly of small isodiametric or slightly elongated (palisade) cells. Palisade cells irregularly distributed, their frequency varying in different species; sometimes arranged in definite layers. Base of the leaf in *Elatine* containing a lacunar

tissue, but with the mesophyll so much reduced or even lacking towards the apex that the upper and lower epidermis are contiguous. Vascular bundles of the **veins** generally surrounded by loose or compact parenchymatous cells in *Bergia*, but **canals** present in this region in a few species; accompanied by sclerenchyma only in a few species of *Bergia*. Vessels arranged in more or less radial rows. **Secreted material** see 'Summary'.

AXIS

STEM

Stem of *Elatine* often irregular in outline as seen in transverse section, owing to the presence of elongated hair-like cells. Suberized cells sometimes present on the outside of old stems of *Bergia*. **Cortex** frequently containing lacunae, especially in aquatic species of both genera, but their size and distribution are said to be of considerable specific diagnostic value. **Endodermis** clearly defined, consisting of thin-walled, or more rarely, of thick-walled cells. **Xylem** exhibiting growth rings in old stems of *Bergia*. Vessels mostly somewhat quadrangular and arranged in radial rows as seen in transverse sections; perforations simple; thickening spiral or annular in the primary xylem, but with horizontally elliptical pits in older material. **Pith** lacking in nearly all species of *Elatine*. **Secretory cells** with tanniferous contents recorded by Sabnis (1977) in the cortex or pith of *Bergia*. For other secreted material see 'Summary'. Secreted material said by Niedenzu (1595) to be particularly abundant in the phloem. Cluster **crystals** of calcium oxalate sometimes occur in the region of the endodermis and in the pith cells of *Bergia*.

Three types of stem structure have been recognized by Pottier (1735) in different groups of *Bergia* spp. (i) Plant glabrous; cortical intercellular spaces very large; fibres absent from the pericycle; pith cells elongated and somewhat resembling phloem as seen in longitudinal section. (ii) Cortical lacunae small; pericyclic fibres present; endodermis well developed and provided with casparian thickenings. (iii) Cortex consisting entirely of assimilatory tissue.

ROOT

Central vascular cylinder (with very variable diameter in different species of *Bergia*, greatly reduced in *Elatine*), attached to the epidermis only by filaments of cells, hence becoming easily separated from the surrounding tissues when sections are cut. Endodermis, pericycle, and phloem not well defined.

TAXONOMIC NOTES

The taxonomic position of the family seems to be somewhat uncertain judging from the different positions to which it has been assigned by various authors. By some it is regarded as having affinities with the Caryophyllaceae and by others as being more closely related to the Frankeniaceae and Tamaricaceae. As with other mainly herbaceous plants which are inhabitants of damp localities or even aquatic, the anatomical structure is not very helpful as an index of taxonomic affinity, since the anatomy of the plants is largely correlated with the nature of the environment. The anatomical structure is not very thoroughly known, and it may be that a more complete investigation would throw further light on the subject.

GENERA DESCRIBED

Bergia, Elatine.

LITERATURE

On *General Anatomy*

D'Almeida 536, Niedenzu 1595, Pottier 1735, Sabnis 1977.

47. HYPERICACEAE

(FIG. 39 on p. 166; FIG. 43 on p. 176)

SUMMARY

(i) GENERAL

Herbs, shrubs, or small trees occurring mostly in the tropics, but some species of *Hypericum* extend to North Temperate regions. The genus *Hypericum* itself includes species which exhibit a great diversity of habit forms ranging from slender herbs to large shrubs or small trees. *H. elodes* Linn. is aquatic. Some of the herbaceous species possess an underground rhizome. The most constant anatomical character is the schizogenous **secretory cavities**, which are present in the leaf of all genera, where they appear as opaque or translucent dots. These cavities are filled with an oil containing a pigment which has been shown by Siersch (2096) to consist of an anthocyanidin, probably in part a rhamnose glucoside of pelargonidin. **Secretory canals** are present in the phloem, and sometimes also in the primary cortex, pericycle and pith of the axis, as well as in the petiole and veins of the leaf. A key to the identification of species of *Hypericum* based on the nature and distribution of the secretory cavities has been drawn up by Clos (433). The **leaf** is generally dorsiventral, with **stomata**, each of which is surrounded by 2 or more cells (see 'Leaf'), confined to the lower surface except in rare instances.

The **axis**, in transverse sections, exhibits closed rings of **xylem** and **phloem**, traversed by narrow but well-defined medullary rays. In the herbaceous species the xylem and phloem are relatively narrow, whilst there is a greater development of pith. The **cortex** in *Hypericum* is usually narrow and includes **secretory cells**. Secretory cells also occur in the phloem and pith. The **pericycle** includes a ring of sclerenchymatous fibres which is usually closed. Solitary and clustered **crystals** of calcium oxalate occur.

(ii) WOOD

(a) *Hypericum*

Hypericum differs from the other genera in having very small, spirally thickened vessels, no parenchyma, wholly uniseriate rays, and septate fibres (in some species).

(b) Genera other than *Hypericum*

Vessels medium-sized, often with an oblique pattern, perforations simple, intervacular pitting alternate, pits to ray cells usually similar to the intervacular pitting and sometimes unilaterally compound, members of medium length. **Parenchyma** in continuous apotracheal bands and sometimes vasicentric in addition. **Rays** up to 2-4 cells wide, heterogeneous to homogeneous.

Fibres usually with simple or indistinctly bordered pits, of medium length.
Vasicentric tracheids often present.

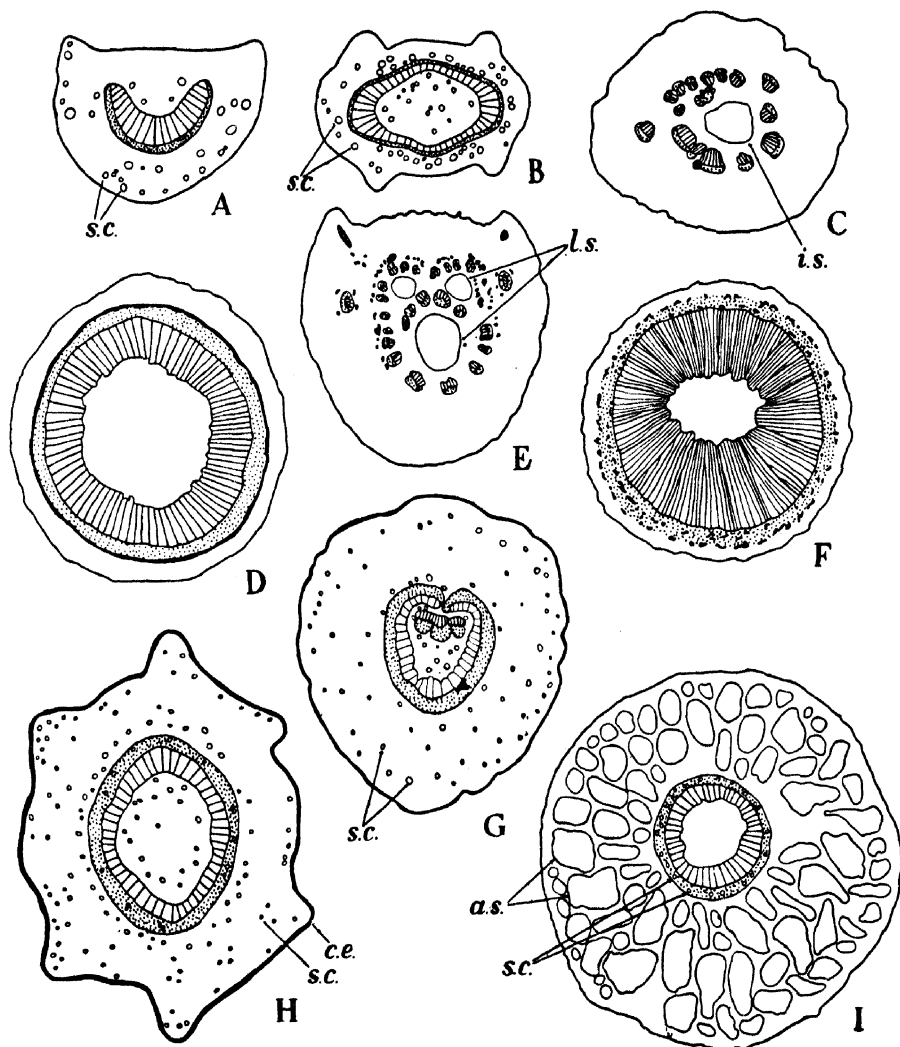


FIG. 39. GUTTIFERAE, A-B and G-H; QUINACEAE, C and E-F;
 HYPERICACEAE, D and I

A, *Calophyllum calaba* Jacq. Petiole $\times 10$. B, *C. calaba* Jacq. Young stem $\times 10$. C, *Quina rhytidopus* Tul. Petiole $\times 15$. D, *Hypericum androsaemum* Linn. Stem $\times 25$. E, *Quina guianensis* Aubl. Petiole $\times 15$. F, *Q. rhytidopus* Tul. Stem $\times 9$. G, *Garcinia mangostana* Linn. Petiole $\times 8$. H, *G. mangostana* Linn. Stem $\times 8$. I, *Hypericum elodes* Linn. Young stem $\times 15$.

c.e. Cutinized epidermis. a.s. Air space. i.s. and l.s. Intercellular spaces. s.c. Secretory canals.

LEAF

Usually dorsiventral. **Hairs** seldom numerous; mostly simple, unicellular or uniseriate; stellate types with uniseriate stalks recorded in certain species of *Harungana*, *Psorospermum*, and *Vismia*. Glandular hairs unknown.

Cuticle frequently thick, especially in species with leathery leaves. **Epidermis** papillose in certain species of *Cratoxylon*, *Harungana*, and *Hypericum*. **Stomata**, confined to the lower surface in most instances; rubiaceous in the *Cratoxyleae* and *Vismieae*, but commonly surrounded by 3 or more cells in *Hypericum*. All types, ranging from a stoma accompanied by 2 cells parallel to the pore to one surrounded by about 9 radially orientated cells, have been recorded in a single leaf of *Hypericum*. **Hypoderm** present in certain species of *Harungana*, *Hypericum*, *Psorospermum*, and *Vismia*. **Mesophyll** usually including a single, but occasionally 2, layers of palisade tissue. **Petiole** of all investigated species exhibiting, in transverse sections, a single arc-shaped vascular strand. For **secretory cavities** and **canals** see 'Summary'. Clustered **crystals** of calcium oxalate present in *Harungana*, *Psorospermum*, and *Vismia*. According to Briquet (272) leaves of certain species of *Hypericum* from arid regions in Brazil have thickened margins consisting of enlarged epidermal cells or collenchyma.

AXIS

YOUNG STEM (Fig. 39 D and I)

Cork generally arising in the pericycle; consisting of alternating layers of unsuberized and uniformly sclerosed cells with fairly wide lumina in *Psorospermum* sp. **Cortex** in woody and semi-woody species of *Hypericum* narrow, consisting of rather loose, small-celled parenchyma when young, but becoming more compact when older. Cortex of the aquatic *H. elodes* Linn. (Fig. 39 I) broad, with abundant intercellular spaces, the structure in transverse sections resembling a network partly composed of secretory idioblasts, the latter being especially numerous at the corners of the meshes. The **endodermis** is well defined in *Hypericum elodes* and, when the stem is sufficiently young, in terrestrial species of the same genus. **Pericycle** containing a sclerenchymatous ring, often closed in certain species of *Cratoxylon*, *Eliaeae*, *Harungana*, *Hypericum*, *Psorospermum*, and *Vismia*, but sclerenchyma absent from the pericycle in certain herbaceous species of *Ascyrum* and *Hypericum* according to Solereder. A ring of fibres, accompanied on the inside by stone cells with thick inner tangential walls, recorded by Solereder immediately beneath the epidermis of *Cratoxylon polyanthum* Korth. **Xylem** and **phloem** forming closed rings in *Hypericum*, but there is a greater development of pith in the herbaceous than in the woody species. Vessels with simple perforations. Cells of the narrow medullary rays filled with secreted material in *Hypericum*. **Secretory canals** (see 'Summary') always present in the secondary phloem (not always very conspicuous), but sometimes occurring also in the pith, pericycle, and outer part of the primary cortex. Their exact position may be of specific diagnostic value according to Clos (433), but the subject needs reinvestigation. Secretory canals are present in the phloem even in species like *Hypericum elodes* (Fig. 39 I) whose structure is specialized in relation to a marshy environment. **Secretory cells**, presumably tanniniferous (stained very darkly with haematoxylin) scattered in the cortex, phloem, and pith of *Hypericum*.

WOOD (Fig. 43 D-G and J)

Vessels typically medium-sized (100–200 μ mean tangential diameter),

but extremely small (less than $25\ \mu$) in *Hypericum*; solitary and in radial pairs, with a distinct oblique, zigzag pattern in *Psorospermum* and *Vismia* (Fig. 43 J) and with a tendency to an oblique arrangement in some species of *Cratoxylon*; sometimes with a tendency to a tangential pattern in *Hypericum*; typically with fewer than 5 vessels per sq. mm., but slightly more numerous in *Vismia* p.p. and sometimes up to 200 or more in *Hypericum*; occasionally with a slight tendency to be ring-porous in *Hypericum*. Perforation plates simple, slightly oblique; Vestal (2329), however, notes scalariform or clustered perforation plates in some species of *Hypericum*. Intervascular pitting alternate, of medium size to rather small; pits to ray cells usually similar to the intervascular pitting, but often elongated and with narrow borders in *Harungana*, and unilaterally compound in some species of *Cratoxylon* and in *Harungana*. Tyloses present in some species, solid deposits sometimes moderately abundant. Mean member length 0.4–0.5 mm. **Parenchyma** in continuous to broken apotracheal bands, 2–6 cells wide in *Cratoxylon* (most species), *Psorospermum* and *Vismia* (Fig. 43 J); similar bands occur in *Harungana*, but tend to link the vasicentric sheaths of tracheids and parenchyma (Fig. 43 F); the bands widely spaced and possibly terminal in *Cratoxylon arborescens* Blume. Parenchyma absent from *Hypericum*. Strands usually of 4 cells, but commonly of 8 cells in some species of *Vismia*; strands with septate crystalliferous cells reported (1886) in *Vismia*. **Rays** up to 4 cells wide in *Psorospermum* and *Vismia* p.p. and tending to be of two distinct sizes in the former, but more commonly only up to 2 or 3 cells wide; all uniseriate in *Hypericum*; less than 1 mm. high and commonly less than 5 cells high in *Hypericum*; uniseriates typically numerous and composed mainly of upright cells, but rather few in some species of *Cratoxylon*, e.g. *C. arborescens*. Usually about 10 rays per mm., but up to 24 in *Hypericum*. Typically heterogeneous (Kribs's Type II A) and commonly with 4–8 marginal rows of upright cells, but with only 1 marginal row or homogeneous in *Cratoxylon*; composed entirely of square and upright cells in the material of *Hypericum* examined, but Vestal (2329) describes the rays of this genus as falling into Kribs's types Heterogeneous II B and III. Silica reported in *Cratoxylon* (794). **Fibres** typically with simple or indistinctly bordered pits that occur mostly on the radial walls, but with distinctly bordered pits in *Psorospermum*. Vestal (2329) notes the occurrence of some septate fibres in *Hypericum*, particularly in the Asiatic species, and has described the formation of the septa in *H. androsaemum* Linn. (2331). Walls thin in *Harungana*, moderately thick to thick in the other genera. Silica reported (794) in *Cratoxylon*. Mean length 1.0–1.4 mm. **Vasicentric tracheids** present in *Harungana*, some species of *Hypericum* (2329) and *Vismia*, and less abundantly in *Cratoxylon*; together with very small vessels, and sometimes parenchyma, they form a matrix linking together and surrounding groups of larger vessels (Fig. 43 F and J).

ROOT

Secretory canals present in the pericycle and secondary phloem of *Hypericum*.

ANOMALOUS STRUCTURE

Bausch's (154) reference to included phloem in *Hypericum* appears to be an error.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The family is very homogeneous, and has many characters in common with the Guttiferae. In fact the Hypericaceae are treated as a tribe of the Guttiferae in Engler's system. The family also has affinities with the Theaceae, although secretory canals are lacking in the Theaceae.

(ii) FROM WOOD STRUCTURE

The genera other than *Hypericum* have characters in their wood anatomy, such as a diagonal pattern of the vessels and the occurrence of vasicentric tracheids that strongly suggest a close relationship with the Guttiferae-Calophylloideae.

Hypericum itself, however, has little in common with this tribe. Its septate fibres resemble those of the Clusiaceae, but apart from this there is not much positive evidence of relationship; the wood of *Hypericum* is much more highly specialized than that of the Clusiaceae.

Vestal (2329) regards the Hypericaceae and Guttiferae as obviously closely related and agrees with Engler, Wettstein, and others in considering them as parts of the same family. On the basis of the wood anatomy and embryo structure Vestal supports Hochreutiner's combination of the two groups through *Psorospermum* and the tribes Calophylloideae and Clusioidae of the Guttiferae, and regards *Hypericum* and its near relatives as derived from the Clusioidae, and the arborescent Hypericaceae from the Calophylloideae.

ECONOMIC USES

Species of *Hypericum* are commonly cultivated for ornamental purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Ascyrum, Cratoxylon, Eliaeae, Harungana, *Hypericum*,* *Psorospermum*, *Vismia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Harungana, *Hypericum* (*Psorospermum*), *Vismia*.

LITERATURE

(i) *On General Anatomy*

Briquet 272, Clos 433, Siersch 2096, Starr 2188, Vestal 2329, 2331.

(ii) *On Wood Structure*

Bailey 100, Bausch 154, Cooper 461, Desch 574, Foxworthy 705, Giordano 786, Gonggrijp 794, Janssonius 1154, Kribs 1283, Lecomte 1334, Record 1843, 1851, Record and Hess 1886, Vestal 2329, 2331, Williams 2430.

48. GUTTIFERAE

(FIG. 39 on p. 166; FIG. 40 on p. 170; FIG. 41 on p. 172; FIG. 42 on p. 174; FIG. 43 on p. 176; FIG. 44 on p. 182; FIG. 49 on p. 208)

SUMMARY

(i) GENERAL

A family of tropical trees and shrubs with rather uniform anatomical structure, and which are characterized especially by the presence in all species of **schizogenous secretory receptacles**, usually in the form of canals, but less frequently of cavities. The canals in the axis are most commonly situated in the pith and primary cortex, but more rarely in the primary or secondary phloem as well. When present in the leaf they may accompany the vascular

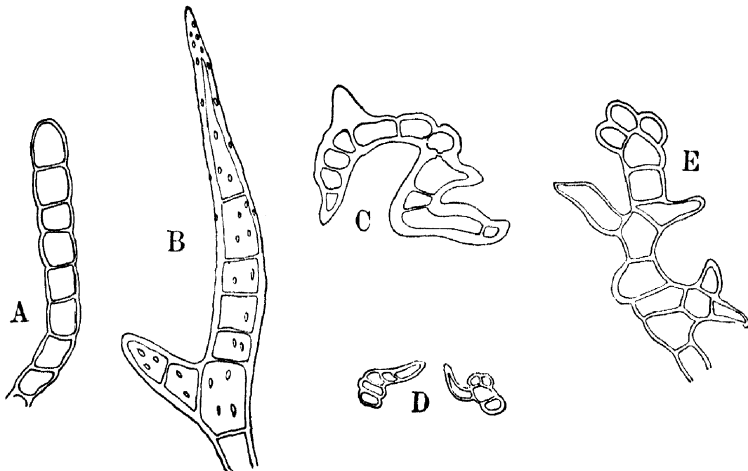


FIG. 40. GUTTIFERAE

Hairs of: A, *Calophyllum retusum* Wall.; B, *C. bracteatum* Thw.; C, *C. pseudotacamahaca* Tr. et Pl.; D, *C. calaba* Jacq. (buds); E, *C. tomentosum* Wight.—After Vesque.

bundles or run independently of them in the mesophyll. They also occur in the petiole. The canals are replaced by secretory cavities in the leaf of certain species. The distribution of the canals and cavities is of some value for the identification of genera and species, but De Cordemoy (469) has shown that allowance must be made for variations within a species in response to environmental and especially to soil conditions. **Secretory cells**, which are readily stained with haematoxylin, are common in the parenchymatous tissues and ray cells of young stems. **Hairs** (Fig. 40) are rare in the family, and where present consist of simple unicellular or uniseriate trichomes, which are more rarely branched or dichotomously divided. Stellate hairs are also known from a few genera. **Stomata** are rubiaceous. The **xylem** and **phloem** in young stems appear, in transverse sections, in the form of continuous rings traversed by narrow rays. **Crystals** of calcium oxalate are usually solitary or clustered, or more rarely in the form of small prisms. They occur fairly widely in the parenchymatous tissues. **Anomalous structure** recorded in *Endodesmia*.

(ii) Wood

Group A (Clusiace)

Vessels often in small multiples, perforation plates simple or simple and scalariform, intervacular pitting and pits to ray cells scalariform, members moderately long to very long. **Parenchyma** paratracheal, sometimes accompanied by diffuse. **Rays** 4–9 cells wide, high, markedly heterogeneous. **Fibres** commonly septate, with simple or slightly bordered pits, moderately long. Without **vasicentric tracheids** or **intercellular canals** in the rays.

Group B (Calophylloideae)

Vessels exclusively solitary, often with a diagonal pattern, perforations simple, intervacular pitting alternate, pits to ray cells commonly elongated, members of medium length. **Parenchyma** apotracheal, in broad bands or diffuse. **Rays** narrow (1–3 cells wide) and low, heterogeneous. **Fibres** with bordered or simple pits, of medium length. **Vasicentric tracheids** nearly always present. **Intercellular canals** occasionally present in the rays.

The genera of the Moronoideae and Garcinieae are intermediate, but tend to be most like Group B, though lacking the characteristic vessel pattern and vasicentric tracheids. In the Kielmeyeroideae some genera resemble Group A, others Group B.

LEAF

Dorsiventral in most species; centric or sub-centric in certain species of *Calophyllum*, *Clusia*, *Garcinia*, *Kielmeyera*, *Moronobea*, *Pentadesma*, *Platonia*, *Rheedia*, *Symphonia*. **Hairs** infrequent or even absent; for types see 'Summary'. Stellate but unicellular trichomes recorded in *Caraipa* (Fig. 49 B) and *Marila*. **Cork warts** recorded in *Clusia* sp. and *Xanthochymus* sp. The height of the cells of the **epidermis**, the thickness of the **cuticle** and degree of undulation of the anticlinal walls of the epidermal cells are somewhat variable and valuable only for the identification of species. The thickness of the cuticle is often considerable. Epidermal cells with marginal pits in the lateral walls recorded in certain species of *Garcinia*, *Kayea*, *Mammea*, *Mesua*, *Pentadesma*, *Platonia*, *Poeciloneuron*, *Rheedia*, *Tovomitia*. Lower epidermis papillose in certain species of *Garcinia*. Some of the epidermal cells horizontally divided in *Calophyllum inophyllum* Linn. **Stomata** (Fig. 41 c) confined to the lower surface, except in certain species of *Garcinia*; rubiaceous. Subsidiary cells filled with a brown homogeneous substance in *Calophyllum inophyllum*; papillose in certain species of *Chrysochlamys* and *Garcinia*. **Hypoderm** of one to several layers common on the upper side of the leaf, especially in *Calophyllum*, *Chrysochlamys*, *Clusia*, *Garcinia*, *Havetia*, *Kielmeyera* (in *K. petiolaris* Mart., but not all other species of *K.*; hypoderm cells thick walled and pitted in this genus), *Montrouzieria*, *Oedematopus* (spongy, Fig. 41 B), *Pilosperma*, *Platonia*, *Quapoia*, *Tovomitia*. **Mesophyll** tending to be sclerotic in several genera. Palisade tissue with reticulately thickened walls, almost prosenchymatous in shape in *Clusia rosea* Linn. (Fig. 41 A). Storage tracheids recorded by Solereder in the leaf tissue of *Endodesmia*. Vascular bundles of the smaller **veins** accompanied or surrounded by sclerenchyma, except in a few species of *Garcinia*; embedded in the mesophyll in a majority of the genera, but vertically transcurrent in *Calophyllum*, *Caraipa*, *Kayea*, *Kielmeyera*, *Mammea*, *Marila*, *Poeciloneuron*. **Petiole**

examined in only a few species, but in these exhibiting, in transverse sections, six more or less distinct types of vascular structure. (i) With a single, arc-shaped vascular strand open on the adaxial side and not accompanied by sclerenchyma in *Calophyllum calaba* Jacq. (Fig. 39 A). (ii) As (i) but ends of the arc-shaped strand incurved and nearly meeting to form a closed tube in species of *Clusia*, *Garcinia*, *Haploclathra leiantha* Benth. (iii) Main vascular strand in the form of a sinuous but completely closed cylinder in *Rheedia laterifolia* Linn. (iv) Main vascular strand forming an almost closed tube surrounding two collateral bundles in *Mammea* sp. (v) As (iv) but main strand forming a completely closed tube surrounding a few collateral bundles

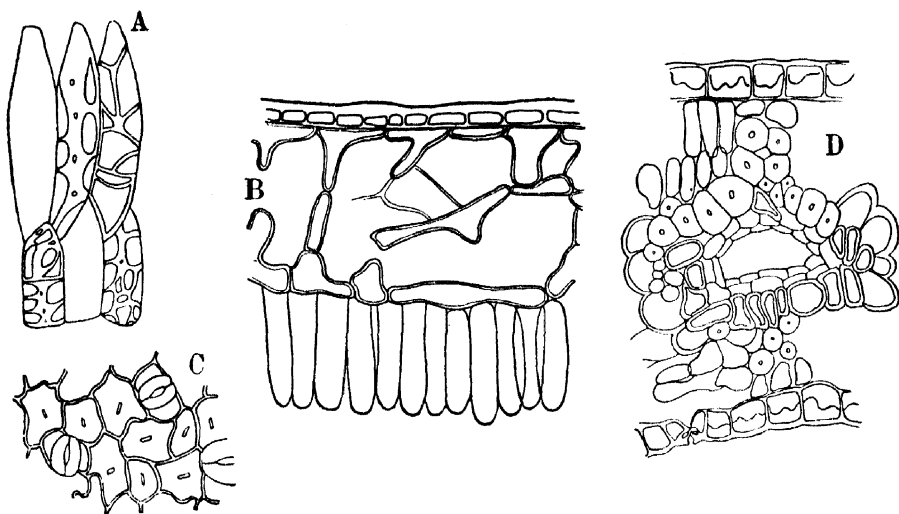


FIG. 41. GUTTIFERAE

A, Group of palisade cells from the mesophyll of *Clusia rosea* L. in a transverse section. B, Spongy, hypoderm from the leaf of *Oedematopus obovatus* Tr. et Pl. C, Crystal-containing epidermis of the leaf of *Garcinia punctata* Oliv. D, Transverse section through the leaf of *Calophyllum buxifolium* Vesque, with a resin-canal accompanied by tracheids and sclerenchymatous fibres.—A, by Solereder, the remainder after Vesque.

in *Garcinia mangostana* Linn. (Fig. 39 G), *Haploclathra paniculata* Benth., and *Mahurea palustris* Aubl.; or with a closed ring surrounding a solitary strand in *Caraipa laxiflora* Benth. and *Kielmeyera petiolaris* Mart. (vi) Main strand in the form of two superimposed U's in *Marila racemosa* Swartz.

Crystals of calcium oxalate usually present in the mesophyll in the form of clusters. Solitary as well as clustered crystals present in *Calophyllum*, *Garcinia* (Fig. 41 C), *Kayea*, *Rheedia*. Crystals exclusively solitary in *Mammea*, *Mesua*, *Pentadesma*, *Poeciloneuron*. Small, usually prismatic crystals occur in many species of *Garcinia*. **Secretory canals** or **cavities** universally present, sometimes appearing as transparent lines or dots when examined with a lens, or with the naked eye. Canals either following the vascular bundles (Fig. 44 E) or running independently of them in the mesophyll; in the latter case sometimes (*Calophyllum*) accompanied by peculiar bundles of tracheids and by sclerenchyma (Fig. 41 D). They also pass through the 'cortical' and 'medullary' regions of the petiole. The nature, size, and distribution of the secretory

canals or cavities are valuable for the identification of species, after making due allowance for variations in response to environmental conditions.

AXIS

YOUNG STEM (Fig. 39 B and H)

Epidermis with a thick cuticle or sclerosed in certain species of *Clusia*, *Garcinia*, *Mammea*, and probably in other genera as well. **Cork** arising immediately below the epidermis in all examined species of *Calophyllum*, *Caraipa*, *Clusia*, *Endodesmia*, *Haploclathra*, *Havetiopsis*, *Kielmeyera*, *Mahurea*, *Mesua*, *Oedematopus*, *Pilosperma*, *Platonia*, *Tovomita*. Outer tangential and radial walls of component cells strongly thickened in *Endodesmia*. **Cortex** commonly containing sclerosed cells; a ring of stone cells present in *Mesua ferrea* Linn. Sclerosed cells not recorded in the cortex of *Marila racemosa* Swartz. An **endodermis** consisting of large, starch-containing cells, recorded in *Kielmeyera*. **Pericycle** recorded as having or observed to include isolated bundles of fibres in certain species of *Calophyllum*, *Garcinia*, *Mammea*, *Rheedia*, *Symphonia*, *Tsimatimia*; but many genera and species, including those of the Kielmeyeroideae, are provided with a composite, continuous ring of sclerenchyma. Both types probably occur in stems of different ages belonging to the same species. **Xylem** and **phloem** appearing, in transverse sections, in the form of continuous rings, traversed by narrow rays in all species which have been examined, notably in *Calophyllum*, *Clusia*, *Garcinia*, *Mammea* as represented in the Kew slide collection. Phloem including fibres in *Caraipa* and *Marila*. Vessels in young twigs seldom more than $50\ \mu$ in diameter, solitary or in short radial groups; perforations simple. Wood fibres arranged in radial rows in *Marila*; very thick walled in *Mahurea*. Pith, apart from canals, &c., composed of cellulose cells in some species but somewhat lignified in others. **Secretory canals** universally present in the primary cortex and pith, and often in the phloem as well, although the canals in the phloem are usually smaller and less conspicuous than those elsewhere. Canals stated to be absent from the phloem in *Allanblackia*, *Clusia*, *Havetiopsis*, *Oedematopus*, *Pentadesma*, *Pilosperma*, *Tovomita*; present in the secondary phloem in *Mammea*; those in the perimedullary region of *Kielmeyera*, *Mahurea*, *Marila*, and in the pericycle of *Mahurea apalustris* Aubl. specially large. Secretory canals sometimes rendered obscure owing to the protrusion of the epithelial cells into the cavity in a manner resembling tyloses in vessels. **Secretory cells**, readily stained with haematoxylin, common in the parenchymatous tissues, notably in species of *Calophyllum*, *Clusia*, *Rheedia*, and probably in other genera as well.

WOOD

(a) *Group A. Clusia Type* (Fig. 42 A-D)

Clusiaceae: *Chrysochlamys*, *Clusia*, *Havetiopsis*, *Tovomita*, and *Tovomitopsis*.

Vessels usually medium-sized ($100\text{--}200\ \mu$ mean tangential diameter), but moderately small ($50\text{--}100\ \mu$) in *Tovomita* and *Tovomitopsis*; solitary and in small multiples, without any pattern; usually 10–14 per sq. mm. Perforation plates all simple or simple and scalariform; some scalariform plates, usually with numerous, fine bars, present in at least some species of *Chrysochlamys*, *Clusia*, *Tovomita*, and *Tovomitopsis*. Intervascular pitting scalariform. Pits

to ray cells almost all elongated horizontally. Solid deposits sometimes abundant. Mean length 0.9–1.2 mm. **Parenchyma** typically paratracheal, vasicentric; tending to be aliform in *Tovomitopsis* and with some scattered cells; sometimes scanty, e.g. in *Chrysochlamys* and *Tovomitopsis* (Fig. 42 A). Gum-like deposits abundant; chambered crystals rather rare; druses, contained in

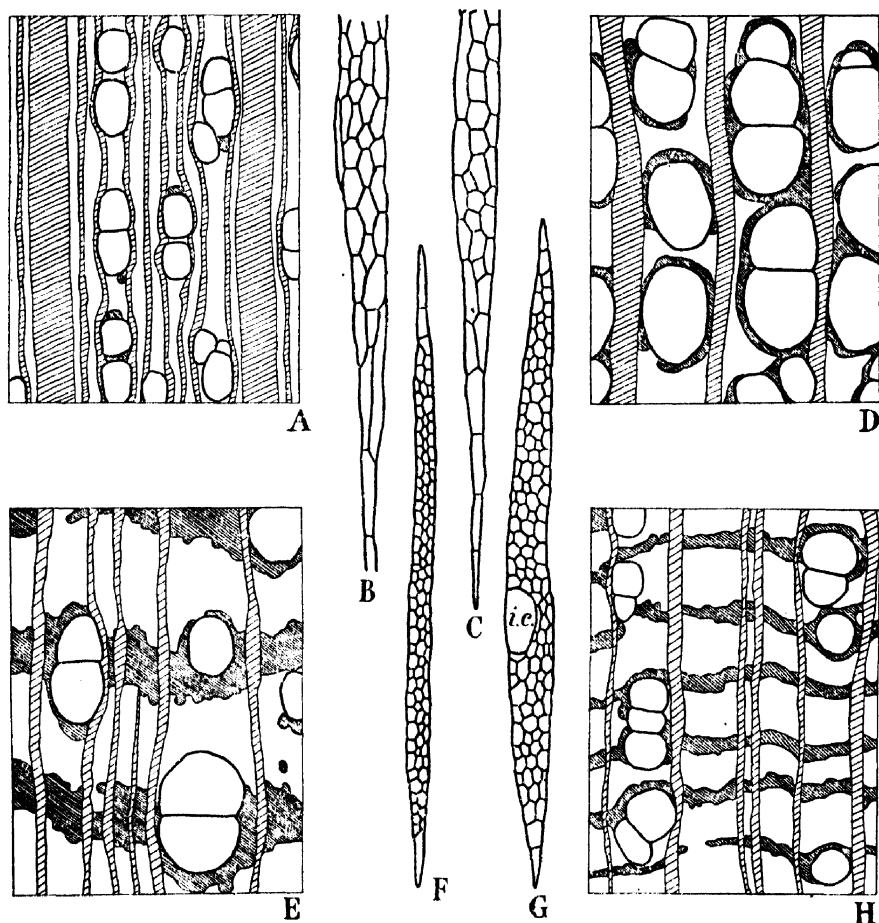


FIG. 42. GUTTIFERAE (Group A and miscellaneous)

A, *Tovomitopsis multiflora* Standl. B, *Clusia cooperi* Standley. C, *Tovomitopsis multiflora* Standl. D, *Clusia odorata* Seem. E, *Symphonia globulifera* Linn. F, *Garcinia mannii* Oliv. G, *Rheedea edulis* Planch. et Triana. H, *Garcinia rostrata* Hassk.

i.c. Intercellular canal.

dilated cells, present in *Clusia*. **Rays** usually of two distinct widths, the larger up to 4–9 (mostly 4–6) cells wide and typically more than 1 mm. high (often considerably more than 2 mm.); uniseriates typically numerous and composed of high upright cells, but very rare in *Havetiopsis*; 5–15 rays per mm.; markedly heterogeneous (Kribs's Type I), with many marginal rows of high upright cells, the cells sometimes all square or upright, e.g. in *Clusia* and

Tovomitopsis (Fig. 42 B and C), and the upright cells in the latter very high in proportion to their width. Typically with abundant gum-like deposits. **Fibres** septate in *Chrysochlamys*, *Clusia*, *Havetiopsis*, and *Tovomitopsis*. Pits simple or with minute borders, and more numerous on the radial than on the tangential walls. Walls thick to extremely thick. Mean length 1.4–1.9 mm.

Mahurea and *Marila*, of the Kielmeyeroideae, appear to have closer affinities with this than with the *Calophyllum* group. *Caraipa* and *Haploclathra*, on the other hand, resemble the latter type and are described with it. *Marila* is outstanding in having septate fibres distributed like diffuse and banded parenchyma among fibre-tracheids with numerous bordered pits. The main points of interest or of difference between *Mahurea* and *Marila* and the genera of Group A are given below.

Vessels smaller and more numerous in *Marila*; rare scalariform plates sometimes present in *Marila*; intervascular pitting alternate; pits to ray cells small and circular; mean member length in *Marila* 0.8 mm. **Parenchyma** absent from *Mahurea* and rare in *Marila*. **Rays** seldom much more than 1 mm. high. **Fibres** septate in *Mahurea* and with some septate fibres in *Marila*, the other fibres in *Marila* with numerous, distinctly bordered pits on both radial and tangential walls; mean length in *Marila* 1.5 mm.

(b) *Group B. Calophyllum Type* (Fig. 43 H–I, K–O)

Calophylloideae: *Calophyllum*, *Kayea*, *Mammea*, *Mesua*, and *Poeciloneuron*.

Vessels usually medium-sized (100–200 μ mean tangential diameter) and sometimes slightly larger; rather smaller in *Kayea*; almost exclusively solitary; with a marked oblique pattern in *Calophyllum* and *Mesua*, and sometimes in *Mammea africana* Sabine (Fig. 43 O); usually about 5 per sq. mm., but more numerous (10–50) in *Kayea*. Perforations typically simple and slightly oblique, but Record and Hess (1886) note a few scalariform plates in *Mammea*. Intersvascular pitting rare, alternate; pits to tracheids moderately large; pits to ray cells commonly elongated and simple, with the long axes horizontal or axial, and sometimes unilaterally compound; Record (1793) has reported 'cribriform membranes' in *Calophyllum*, but, according to Bailey (78), these are not true vested pits. Tyloses sometimes abundant, sclerosed in *Mesua*; solid deposits sometimes present. Mean length 0.4–1.0 mm. **Parenchyma** in broad, often widely spaced apotracheal bands in *Calophyllum*, *Kayea*, and *Mesua* (Fig. 43 K); the bands sometimes locally discontinuous and showing some tendency to association with the vessels; diffuse in *Mammea* (Fig. 43 O); predominantly paratracheal in *Poeciloneuron*, sheathing the vessels on the abaxial sides and extending as long, narrow wings (unilaterally paratracheal). Chambered crystalliferous cells usually present and often abundant. Strands typically of 8 cells. **Rays** usually up to 2–3 cells wide, but exclusively uniseriate in *Mesua* and most species of *Calophyllum*; sometimes 4–5 cells wide in *Mammea*; less than 1 mm. high; uniseriates numerous, usually composed of both upright and procumbent cells; 8–17 rays per mm.; heterogeneous (Kribs's Type II B), with 1–4 (occasionally more) marginal rows of square to upright cells; commonly with more than 4 marginal rows in *Mammea africana* and the uniseriates composed of upright cells only. Gum-like deposits abundant. **Fibres** with numerous bordered pits on both radial and tangential walls in *Kayea*, *Mammea*, and *Poeciloneuron*, the borders conspicuous in

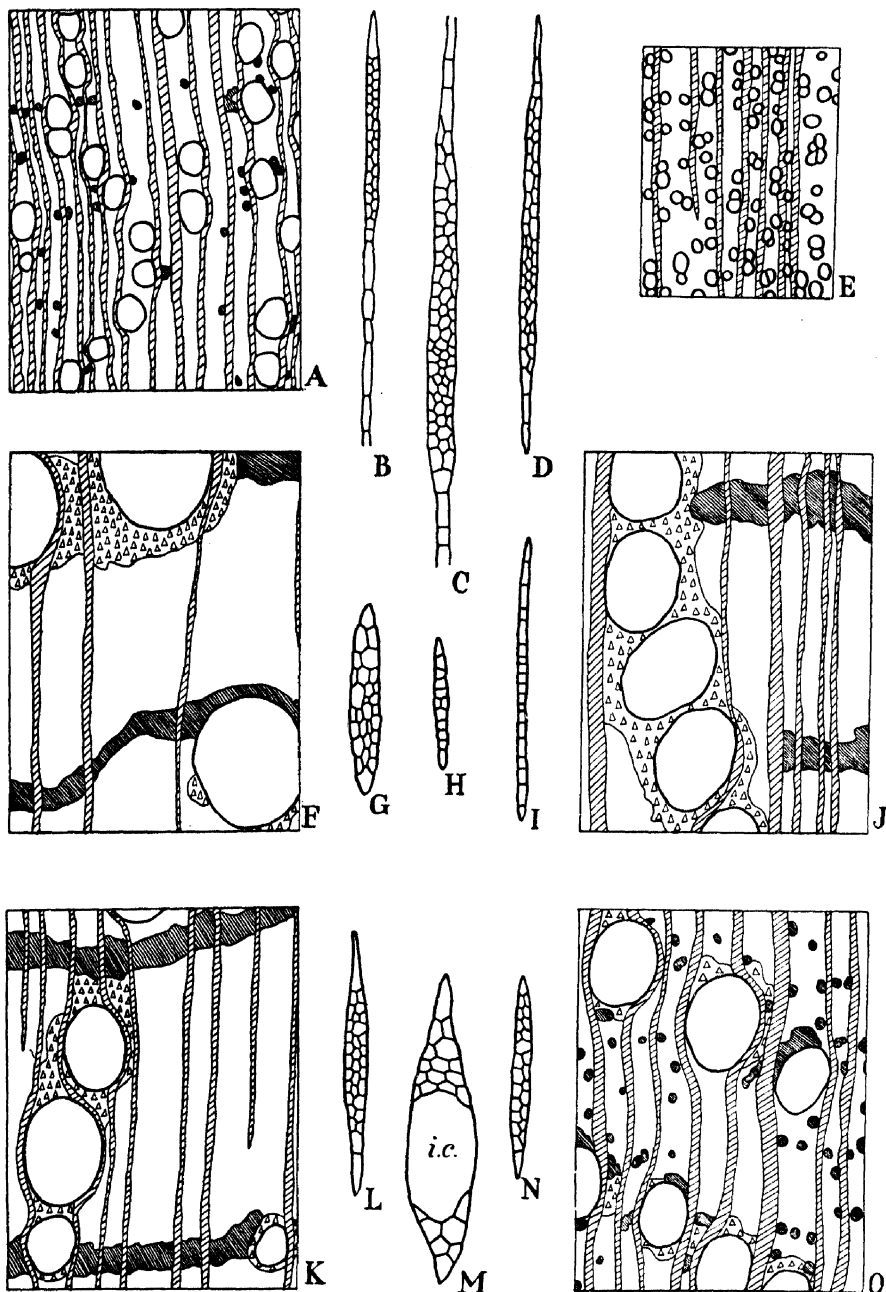


FIG. 43. QUIINACEAE, A-C; HYPERICACEAE, D-G and J;
GUTTIFERAE (Group B), H-I and K-O

A, *Touroulia guianensis* Aubl. B, *Lacunaria jenmanii* (Oliv.) Ducke. C, *Quina panamensis* Standl. D, *Vismia latifolia* Chois. E, *Hypericum acerosum* H. B. et K. F, *Harungana madagascariensis* Lam. G, *Cratoxylon arborescens* Bl. H, *Mesua ferrea* Linn. I, *Calophyllum inophyllum* Linn. J, *Vismia leonensis* Hook. f. K, *Calophyllum wallichianum* Planch. L, *Kayea grandis* King. M, *Mammea africana* Sabine. N, *Poeciloneuron indicum* Bedd. O, *Mammea africana* Sabine.
i.c. Intercellular canal.

Mammea; with small bordered or simple pits on the radial walls in *Calophyllum* and *Mesua*. Walls thick to extremely thick. Mean length 1.0–1.4 mm. **Vasicentric tracheids** with conspicuous bordered pits observed in all the genera; Record and Hess (1886), however, have not recorded tracheids in the New World species of *Mammea*. **Intercellular canals** present in the rays of *Mammea* (Fig. 43 M).

The genera of the Moronoboideae—*Montrouziera*, *Moronobea*, *Pentadesma*, *Platonia*, and *Symphonia*—and of the Garcinieae—*Allanblackia*, *Garcinia*, *Pentaphalangium*, and *Rheedia*—on the whole show greater affinities with this than with the *Clusia* group (A). The main points of interest or of difference from Group B are given below.

Vessels similar except that short radial multiples are moderately common and there is no diagonal pattern, except for a slight tendency in *Pentadesma*. Intervascular pitting medium-sized to large and often with coalescent apertures in the Garcinieae; pits to ray cells not so markedly elongated and all circular in the Garcinieae (except *Garcinia*). Mean member lengths, *Garcinia* 0.3–0.6 mm., *Symphonia* 0.6 mm. **Parenchyma** similar but the bands more numerous and less regular (Fig. 42 H); often more closely associated with the vessels and intermediate between confluent and metatracheal (Fig. 42 E). Chambered crystals common in most of the genera; druses sometimes present in *Garcinia*, e.g. *G. globulosa* Ridl., and *Pentaphyllum*. **Rays** wider (up to 4–6 cells) and distinctly higher; uniseriate few to very few, composed of 1–3 upright cells, procumbent cells only or mixed procumbent and upright cells; rays varying from distinctly heterogeneous (Kribs's Type II B) with 1–4 marginal rows of upright cells, e.g. in *Garcinia mannii* Oliv., to almost homogeneous (Kribs's Type I), e.g. in *Allanblackia* and *Garcinia holtumii* Ridl. Silica reported (794) in *Garcinia*. **Fibres** with simple pits, more common on the radial than on the tangential walls. Mean lengths, *Garcinia* 1.3–2.0 mm., *Symphonia* 1.7 mm. **Vasicentric tracheids** absent. **Intercellular canals** present in the rays of *Rheedia* (Fig. 42 G).

Caraipa and *Haploclathra* of the Kielmeyeroideae appear from descriptions to be closely related to this group; both have a tendency to oblique lines of vessels, almost exclusively uniseriate rays and parenchyma that is described (1886) as unilaterally paratracheal with short to long extensions; *Caraipa* has solitary vessels, fibres with distinctly bordered pits and vasicentric tracheids. **Interxylary (included) phloem** see below.

ANOMALOUS STRUCTURE

Anomalous structure of the foraminat type (*corpus lignosum foraminulatum*) noted by Pfeiffer (1712) in *Endodesmia*.

ROOT

Secretory canals, similar to those of the stem, present in the cortex alone or in the cortex and phloem in certain species of *Calophyllum*, *Clusia*, *Garcinia*, *Mammea*, *Rheedia*, *Xanthochymus*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The anatomy of the leaf and young stem is fairly uniform throughout the Guttiferae. In spite of the fact that some botanists regard the Kielmeyeroideae

as rather distinct from the remainder of the family on the basis of their external morphological characters, there does not appear to be any corresponding demarcation in the structure of the leaf and shoot so far as these have been investigated. Similarly the Hypericaceae have many points in common with the Guttiferae and it seems to be largely a matter of opinion whether the Hypericaceae should be treated as a distinct family or as a tribe of the Guttiferae. The Theaceae are distinguished from the Guttiferae in lacking secretory canals, but it is interesting to note that canals occur in the Dipterocarpaceae.

(ii) FROM WOOD STRUCTURE

Two extreme groups can be distinguished, the Clusiaceae and the Calophylloideae, the former having distinctly more primitive vessel and ray characters. These two groups are more sharply distinguished than are many families.

The Garcinieae and Moronoboideae resemble each other in most characters and have many features in common with the Calophylloideae, though lacking the characteristic vessel pattern and vasicentric tracheids of this group. Though they have been placed with the Calophylloideae, it should be borne in mind that they also have characters in common with the Clusiaceae and that at least some of the difference might be accounted for as the result of the higher level of specialization in the Garcinieae and Moronoboideae.

The Kielmeyeroideae appears to be a mixed group. *Mahurea* and *Marila* have many features in common with the Clusiaceae, whereas *Caraipa* and *Haploclathra* closely resemble the Calophylloideae.

Mammea differs from all the other genera of the Calophylloideae in having diffuse parenchyma.

ECONOMIC USES

The timbers are not generally of great commercial importance, though some are very well known locally. The most important genus is *Calophyllum*, the woods of which are characteristically strong and durable. The best-known species are *C. brasiliense* Camb., which is widely used in South America for general construction, shipbuilding, furniture, and other purposes, *C. calaba* Jacq., the Santa Maria of Central America, *C. inophyllum* Linn., the Palo Maria of the Philippines and Poon of India, and *C. tomentosum* Wight, Poon or Poonspar from India, which is used for masts and spars and for a variety of other purposes. The timber of *Mesua ferrea* Linn. is very strong and durable and has a high reputation in India for railway sleepers, bridging, and heavy construction. General utility timbers are provided by some of the other genera, such as *Kayea* and *Symphonia*.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Allanblackia, Calophyllum,* Caraipa, Chrysochlamys, Clusia,* Garcinia,* Haploclathra, Havetia, Havetiopsis, Kayea, Kielmeyera, Mahurea, Mammea,* Marila, Mesua, Montrouziera, Moronobea, Oedematopus, Pentadesma, Pilosperma, Platonia, Poeciloneuron, Quapoya, Rheedia,* Symphonia, Tovomitia, Tsimatimia, Xanthochymus.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Allanblackia, Calophyllum, (Caraipa), (Chrysochlamys), Clusia, Garcinia, (Haploclathra), Havetiopsis, Kayea, Mahurea, Mammea, Marila, Mesua, (Montrouzieria), Moronobea, Pentadesma, (Pentaphalangium), Platonia, Poeciloneuron, Rheedia, Symphonia, Tovomita, Tovomitopsis.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Brandza 262, Buttrick 325, De Cordemoy 469, Engler 634, Kienholz 1236, Vestal 2329.

(ii) *On Wood Structure*

Bailey 78, Bausch 154, Beekman 167, Benoist 169, den Berger 180, Besson 186, Burgerstein 310, Chalk 364, Cooper 461, Dadswell 525, Dadswell and Record 533, Demougeot 563, Desch 574, Foxworthy 705, Garratt 748, Gonggrijp 794, Greene 809, Janssonius 1147, 1154, Jentsch 1171, 1178, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Méniard 1491, Pearson and Brown 1679, Pereira 1687, Pfeiffer, H. 1712, Pfeiffer J. Ph. 1713, Record 1793, 1801, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2206, 2207, Tang 2231, Torres 2269, Vestal 2329, Webber 2377.

49. QUIINACEAE

(FIG. 39 on p. 166; FIG. 43 on p. 176)

SUMMARY

(i) GENERAL ANATOMY

A small family of trees, shrubs, and climbers from tropical America. The family is usually regarded as having affinities with the Guttiferae, but differs from them in lacking schizogenous canals with resinous contents, and in possessing lysigenous intercellular spaces filled with mucilage, notably enclosed within the vascular strand of the midrib and petiole. The venation of the leaf has a feathery appearance in herbarium specimens, and this is caused by the sheath of very thick-walled fibres by which the vascular bundles are surrounded, some of the fibres extending into the mesophyll or lying immediately below the epidermis parallel with the surface of the leaf.

(ii) WOOD

Vessels mostly solitary, occasionally with a slight radial or oblique pattern, perforations simple, intervacular pitting alternate and very small, pits to ray cells similar, members moderately to very long. **Parenchyma** apotracheal, diffuse; reported to be sometimes predominantly paratracheal; sometimes septate. **Rays** up to 2-4, or rarely 5-6, cells wide, high, markedly heterogeneous. **Fibres** with distinctly bordered pits, moderately long. **Vasicentric tracheids** occasionally present.

LEAF

Dorsiventral. **Hairs** infrequent. Cells of the upper **epidermis** polygonal, straight sided, but with thickenings of the cell wall projecting into the lumen. Anticlinal walls of the cells of the lower epidermis rather unevenly thickened. **Stomata** confined to the lower surface, up to about 20 μ in longitudinal diameter (surface view); rubiaceous. **Mesophyll** composed of 2 layers of

palisade cells in *Q. rhytidopus* Tul., but of only one layer in *Q. guianensis* Aubl., together with a broader layer of spongy tissue consisting of small cubical cells in both species. All vascular bundles of the **veins**, especially the smaller ones, surrounded by sheaths of very thick-walled fibres with branches from the latter extending into the mesophyll and sometimes lying beneath the epidermis parallel with the surface of the leaf. **Midrib** with an annular vascular strand, flattened or slightly concave towards the adaxial surface, enclosing a collateral, medullary bundle. **Petiole** of *Q. rhytidopus* (Fig. 39 c), in transverse sections through the distal end, exhibiting an interrupted ring of collateral bundles accompanied by 2 additional strands in the cortical region. There is a large secretory cavity enclosed within the main vascular strand. Petiolar structure similar in *Q. guianensis* (Fig. 39 e) but with an accessory arc of medullary vascular strands as well as 1 large and 2 small secretory cavities, the larger one being on the concave side and the 2 smaller ones in the convex side of the arc of medullary strands. Cluster **crystals** present in the petiole and mesophyll of both species. **Secretory cells** with amorphous contents observed in *Q. rhytidopus*. For **secretory cavities** see 'Petiole' above.

AXIS

YOUNG STEM (Fig. 39 f)

Cortex containing occasional groups of thick-walled, pitted stone cells. **Pericycle** including groups of thick-walled fibres. **Phloem** and **xylem** in the form of closed cylinders, traversed by uniseriate medullary rays. Small groups of thick-walled fibres scattered throughout the phloem. Vessels solitary and in radial groups, up to about 50 μ in radial diameter; perforations simple, oblique. Groundwork of the wood composed of radial rows of very thick-walled fibres, the inner part of the walls being clearly demarcated from the outer portion. **Pith** composed of pitted, parenchymatous cells with moderately thick walls. **Secretory cells** with amorphous contents scattered throughout the parenchymatous tissues; more numerous in *Q. guianensis* Aubl. than in *Q. rhytidopus* Tul. Cluster **crystals** also present; especially abundant in the cortex of *Q. guianensis*.

WOOD (Fig. 43 A-C)

Vessels moderately small (mean tangential diameter 50–100 μ); mostly solitary, but with a few radial pairs; sometimes with a tendency towards a radial or oblique pattern, e.g. in *Touroulia guianensis* Aubl.; about 20 per sq. mm. Perforations simple and moderately oblique. Intervascular pitting alternate, very small to minute; sometimes with coalescent apertures (1886); pits to ray cells similar to the intervascular pitting. Solid deposits common. Mean length 0.9–1.3 mm. **Parenchyma** apotracheal in all the material examined, as isolated cells or groups of 2 or 3 scattered among the fibres (diffuse), but Record and Hess (1886) describe the parenchyma as 'paratracheal, sometimes confluent; also diffuse . . .'. Strands usually of 2–4 cells, the individual cells sometimes containing single septa; chambered solitary crystals numerous in *Touroulia guianensis* and rare septate parenchyma containing druses reported (2329) in *Quiina cruegeriana* Griseb. **Rays** up to 2–4 (occasionally 5–6) cells wide and more than 1 mm. high; uniseriates

numerous and composed entirely of upright cells; 17–20 rays per mm.; markedly heterogeneous (Kribs's Type I), commonly with 8 or more marginal rows of upright cells, which often link together 2 or more multiseriate parts. Deposits of gum abundant. **Fibres** with distinctly bordered pits that are equally numerous on both radial and tangential walls; cells in contact with the vessels with very numerous small pits in *Lacunaria*, but not distinctly shorter than the other fibres. Walls very thick. Mean length 1.6–2.1 mm. **Vasicentric** tracheids occasionally present in *Quiina* and *Touroulia*.

TAXONOMIC NOTES

The characters recorded in the 'Summary' seem to provide sufficient justification for separating the Quiinaceae from the Guttiferae. Vestal (2329) considers the wood structure of this family to be at a similar level of development to that of the Guttiferae, but as taking its origin from the Theaceae. The length of the vessel members and the primitive type of ray suggest that it might be regarded as intermediate in this respect between the *Calophyllum* and *Clusia* types of the Guttiferae (see p. 173).

Although in type of parenchyma the Quiinaceae resembles the Theaceae rather than the Guttiferae, and in ray type the Theaceae and the *Clusia* group of Guttiferae rather than the *Calophyllum* group, yet the occasional presence of vasicentric tracheids and of a loose oblique or radial vessel pattern suggest affinity with the *Calophyllum* group of the Guttiferae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

The part dealing with general anatomy is based on a study of specimens of *Quiina guianensis* Aubl.* and *Q. rhytidopus* Tul.* in the Kew Herbarium.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Lacunaria, *Quiina*, *Touroulia*.

LITERATURE

(i) *On General Anatomy*
Engler 634.

(ii) *On Wood Structure*
Record 1843, 1851, Record and Hess 1886, Vestal 2329.

50. THEACEAE

(FIG. 44 on p. 182; FIG. 45 on p. 186; FIG. 46 on p. 192)

SUMMARY

(i) GENERAL

A family of trees and shrubs, often with leathery leaves, which occurs in Tropical Asia and temperate regions in the Far East. **Hairs** infrequent, but where present they are generally unicellular, acuminate, with thick walls. Fasciculate and tufted hairs with unicellular rays have also been recorded.

The leaf is generally dorsiventral with 1–3 layers of palisade tissue. The **epidermis** consists partly or wholly of mucilaginous cells in certain species. **Stomata** are confined to the lower surface; in many genera surrounded by 2–5 narrow, subsidiary cells, more or less distinctly differentiated from the

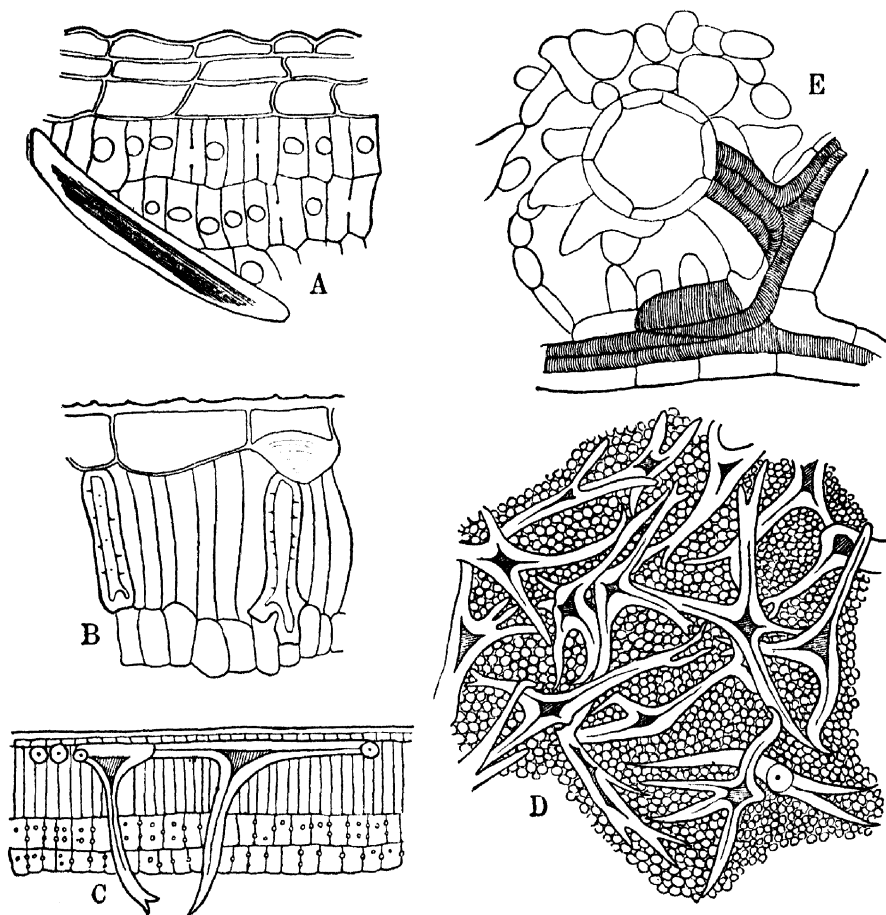


FIG. 44. SAURAUACEAE, A; THEACEAE, B–D; GUTTIFERAE, E

A, Transverse section through part of the leaf (upper side) of *Saurauia nepaulensis* DC, with arm-palisade-parenchyma. B, Part of a transverse section of the leaf of *Freziera undulata* Swartz, with a mucilaginous epidermal cell and with rod-shaped idioblasts. C–D, Idioblasts of *Cleyera grandiflora* Hook. fil. et Thoms.; C, in a transverse section of the leaf; D, in a superficial section of the upper side of the leaf. E, Secretory cavity in a mesh between the veins of *Carapa fasciculata* Camb.: vessels extend from the vascular bundles of the veins to the secretory cavity.—By Solereder.

remaining epidermal cells. In other cases the stomata are ranunculaceous. Sclerenchymatous idioblasts in the parenchymatous tissues of the leaf as well as in the cortex and pith of the axis are especially characteristic of the family. Variations in their size, shape, and frequency are helpful in distinguishing genera and species. (For details see 'Leaf'.) The **petiole** in most genera is characterized, in transverse sections, by a solitary, crescentic vascular strand,

but in some instances small lateral bundles are present as well. Prismatic and clustered **crystals** are common in both leaf and axis. The family may be divided into two distinct groups so far as the seat of origin of the **cork** in young stems is concerned. In one of these its origin is superficial, most frequently sub-epidermal, whilst in the other it arises in the pericycle. Where the cork arises superficially the cortex is relatively broad and durable, the outer part being collenchymatous; but in genera with a deeply seated phellogen it is often narrower, and soon cut off by the formation of cork in the pericycle. The **endodermis** is usually ill defined. The **pericycle** includes heterogeneous sclerenchyma, but becomes entirely sclerified in most of the genera. The **phloem** and **xylem** appear, in transverse sections, as closed rings traversed by narrow rays, and surround the central **pith** which is often heterogeneous and may contain idioblasts and crystals.

(ii) Wood

Vessels typically small, predominantly or exclusively solitary, semi-ring-porous in some species, commonly with spiral thickening, perforation plates very oblique and scalariform, often with many bars, intervascular pitting scalariform or opposite, pits to parenchyma similar, sometimes simple. Members vary to extremely long. **Parenchyma** predominantly apotracheal, diffuse or in short lines, vasicentric present in addition in some genera. **Rays** sometimes of 2 distinct widths, 1-8 cells wide, commonly only up to 2 or 3 cells, moderately short to high, heterogeneous with 3-10 marginal rows of upright cells. **Fibres** with conspicuous bordered pits, of medium length to very long.

LEAF

Generally dorsiventral, and frequently covered by thick **cuticle**. **Hairs** infrequent, but when present unicellular, acuminate, thick walled in *Camellia*, *Eurya*, *Gordonia*, *Nabiasodendron*, *Stewartia*, *Ternstroemiopsis*. Fasciculate hairs with unicellular rays recorded in *Gordonia* and *Ternstroemiopsis*. Tanniniferous **cork warts** present on the lower surface in certain species of *Adinandra*, *Anneslea*, *Camellia*, *Eurya*, *Ternstroemia*. Marginal **hydathodes**, consisting of cells elongated at right angles to the leaf surface, recorded by Lepeschkin (1361) in the leaf teeth of *Camellia japonica* Linn. **Epidermis** including mucilaginous cells in certain species of *Archytaea*, *Camellia*, *Cleyera*, *Eurya*, *Freziera* (Fig. 44 B), *Gordonia*, *Laplacea*, *Nabiasodendron*. **Stomata** almost or completely confined to the lower surface, surrounded by 2-5, narrow subsidiary cells in certain species of *Adinandra*, *Anneslea*, *Camellia*, *Cleyera*, *Freziera*, *Ternstroemia*, *Visnea*; rubiaceous in *Archytaea*; ranunculaceous in some genera. Guard and subsidiary cells lignified in *Camellia* as shown by treatment with phloroglucin and hydrochloric acid according to Heilbronn (932). **Hypoderm** present on the upper side of the leaf in certain species of *Archytaea*. **Mesophyll**. Palisade tissue consisting of 1-3 layers, the number of layers being of some value for the identification of genera and species. Spongy parenchyma occupies half to two-thirds of the mesophyll. Sclerenchymatous idioblasts of various types, sometimes appearing as transparent dots in the leaves, present in the mesophyll of *Adinandra*, *Anneslea*, *Camellia*, *Cleyera* (Fig. 44 C-D), *Eurya*, *Franklinia*,

Freziera (Fig. 44 B), *Gordonia* (extending from the upper to the lower epidermis in the last two genera), *Laplacea*, *Nabiasodendron*, *Pyrenaria*, *Schima*, *Ternstroemia*, *Visnea*. Idioblasts varying in shape in different genera.

- (i) Much thickened and provided with more or less elongated branches with pointed ends in *Anneslea*, *Camellia*, *Franklinia*, *Laplacea*, *Pyrenaria*, *Schima*, *Ternstroemia*.
- (ii) Branched, but with rounded endings to the branches in *Gordonia*.
- (iii) Only slightly branched and thickened, solitary or in groups in *Adinandra*, *Eurya*, *Visnea*.
- (iv) Almost circular or rectangular, slightly thickened and mostly solitary in *Archytaea* and *Ploiarium*.
- (v) In the form of spicular cells traversing the palisade tissue or the whole of the mesophyll in certain species of *Cleyera*, *Freziera*, *Gordonia*, and *Schima*.
- (vi) Absent from *Stewartia* (except the pedicel).

Midrib usually containing a V- or U-shaped vascular strand, surrounded by thick-walled tissue. **Petiole**, in transverse sections through the distal end, exhibiting a solitary, arc-, U-, or V-shaped vascular strand in *Adinandra*, *Anneslea*, *Camellia* (Fig. 46 B) (pro parte, margins of strand frequently incurved), *Cleyera*, *Eurya*, *Freziera* (pro parte), *Laplacea*, *Nabiasodendron*, *Pyrenaria*, *Stewartia*, *Ternstroemia*, *Ternstroemiopsis*, *Visnea*. Large median strand accompanied by several smaller lateral ones in *Anneslea* (base of petiole), *Archytaea*, *Camellia* (pro parte), *Gordonia*, *Lacathea*, and *Schima*. Vascular strand of the petiole closed in certain species of *Freziera*. Idioblasts present, especially in the 'cortex' of the petiole in *Adinandra*, *Anneslea*, *Camellia*, *Cleyera*, *Eurya*, *Franklinia*, *Freziera*, *Gordonia*, *Laplacea*, *Nabiasodendron*, *Pyrenaria*, *Schima*, *Ternstroemia*, *Ternstroemiopsis*, *Visnea*. The development and structure of the idioblasts in the petiolar ground tissue of *Camellia japonica* have recently been investigated by Foster (694). The idioblasts arise from parenchymatous cells with specially large nuclei, and remain uninucleate throughout the life of the protoplast. The cells soon put out 'one or more delicate tubular branches which extend between the walls of neighbouring tissue-elements and may ultimately penetrate certain of the intercellular air-spaces. The continued ramification of the sclereid is accompanied by the origin and development of "spicules" which, like the major branches, grow in between the walls of adjacent parenchyma cells.' A pitted secondary wall is formed around the cell after the intercellular development is complete. Foster suggests that the idioblasts develop by 'intrusive' growth, but concludes that elongation of the major branches is not necessarily restricted to their tips.

'Pericycle' sclerenchymatous in *Anneslea*, *Lacathea*, *Pyrenaria*, *Schima*, *Stewartia* (pro parte), *Ternstroemia* (partly fibrous); collenchymatous in certain species of *Camellia*, *Stewartia*, and *Ternstroemiopsis*. Petiole not well defined in *Archytaea*, owing to the decurrent leaf bases. Solitary prismatic and/or clustered **crystals** of calcium oxalate present in the mesophyll of *Anneslea*, *Cleyera*, *Freziera*, *Stewartia*, *Ternstroemia*, *Visnea*. Sphaero crystalline masses recorded in the epidermis of certain species of *Eurya*. Crystals present in the 'cortex' of the petiole in *Cleyera*, *Eurya*, *Pyrenaria*, *Visnea*.

AXIS

YOUNG STEM (Fig. 46 D-F and L)

Young stem usually circular, but rarely (*Visnia*) quadrangular in transverse sections. **Cork** arising in the sub-epidermis of *Adinandra*, *Anneslea*, *Archytaea*, *Cleyera* (Fig. 46 L), *Eurya*, *Franklinia*, *Freziera*, *Gordonia* (pro parte), *Schima*, *Ternstroemia*, *Visnea*; pericyclic in *Camellia* (Fig. 46 E), *Gordonia* (pro parte), *Laplacea*, *Nabiasodendron*, *Pyrenaria*, *Stewartia*, *Tutcheria*. Cork cells thin-walled in *Anneslea*, *Archytaea*, *Cleyera*, *Eurya*, *Franklinia*, *Freziera*, *Schima*, *Stewartia*, *Ternstroemiopsis* (majority of cells), *Visnea*; with U-shaped thickening in species of *Camellia*, *Laplacea*, *Nabiasodendron*, *Ternstroemia*, *Ternstroemiopsis*. Cells containing tannic substances in *Anneslea* and *Ternstroemiopsis*. Primary **cortex** consisting of up to about 12 layers of cells, outer part frequently collenchymatous, inner part spongy, containing sclerenchymatous idioblasts in *Adinandra*, *Anneslea*, *Cleyera* (Fig. 46 D and F), *Eurya*, *Freziera*, *Laplacea*, *Nabiasodendron*, *Schima*, *Ternstroemia*, *Visnea*. Idioblasts rounded in *Archytaea*; absent from *Stewartia* except from the pedicel, and sometimes from young stems of *Camellia*.

Endodermis indistinct. **Pericycle** varying somewhat according to the age of the shoot; always heterogeneous but entirely sclerified in *Adinandra*, *Archytaea*, *Camellia* (pro parte), *Cleyera*, *Eurya*, *Franklinia*, *Freziera*, *Gordonia*, *Laplacea*, *Nabiasodendron*, *Pyrenaria* (fibre groups becoming separated owing to the action of sub-adjacent phellogen), *Schima*, *Stewartia*, *Ternstroemiopsis*. Pericycle containing isolated groups of fibres in *Anneslea*, *Camellia* (pro parte), *Ternstroemia*, *Visnea*. **Phloem** and **xylem** appearing, in transverse sections, as continuous cylinders traversed by narrow rays. Phloem containing a variable proportion of fibres in different genera. Phloem fibres especially large and thick walled in *Adinandra*, *Anneslea*, *Gordonia*, *Laplacea*, *Pyrenaria*, *Ternstroemia*; usually absent from *Eurya*, *Stewartia* (very young stem), and *Camellia* (very young stem).

Xylem. Vessels usually solitary, up to about 40 μ in diameter; perforation plates scalariform, often with many bars. Perimedullary region frequently sclerified. **Pith** composed exclusively of isodiametric cells in *Pyrenaria*, but more or less heterogeneous in other genera, this character being especially well developed in *Camellia* and *Stewartia*. Pith, when heterogeneous, consisting of a mixture of large thin-walled cells embedded in a network of smaller ones with thicker and sometimes pitted walls. Sclerenchymatous idioblasts sometimes occur in the pith, having been recorded in certain species of *Adinandra*, *Camellia*, *Eurya*, *Franklinia*, *Laplacea*, *Nabiasodendron*, *Schima*, *Visnea*. Idioblasts form diaphragms in the pith in certain species of *Cleyera*, *Eurya*, *Freziera*, *Ternstroemia*, and *Visnea*. Prismatic or clustered **crystals** present in the cortex of *Anneslea*, *Cleyera*, *Eurya*, *Franklinia*, *Freziera*, *Gordonia*, *Stewartia*, *Ternstroemia*, *Ternstroemiopsis*, *Visnea*. Crystals also occur in the phloem of *Eurya* and *Stewartia*.

WOOD (Fig. 45 A-G, K-L, and N)

Vessels typically small (less than 100 μ mean tangential diameter, sometimes very small (25-50 μ), e.g. in species of *Camellia*, *Pyrenaria*, and *Sakakia*, slightly more than 100 μ in some species of *Schima* and *Ternstroemia*, e.g. *S. noronhae* Reinw.; predominantly or exclusively solitary; very variable

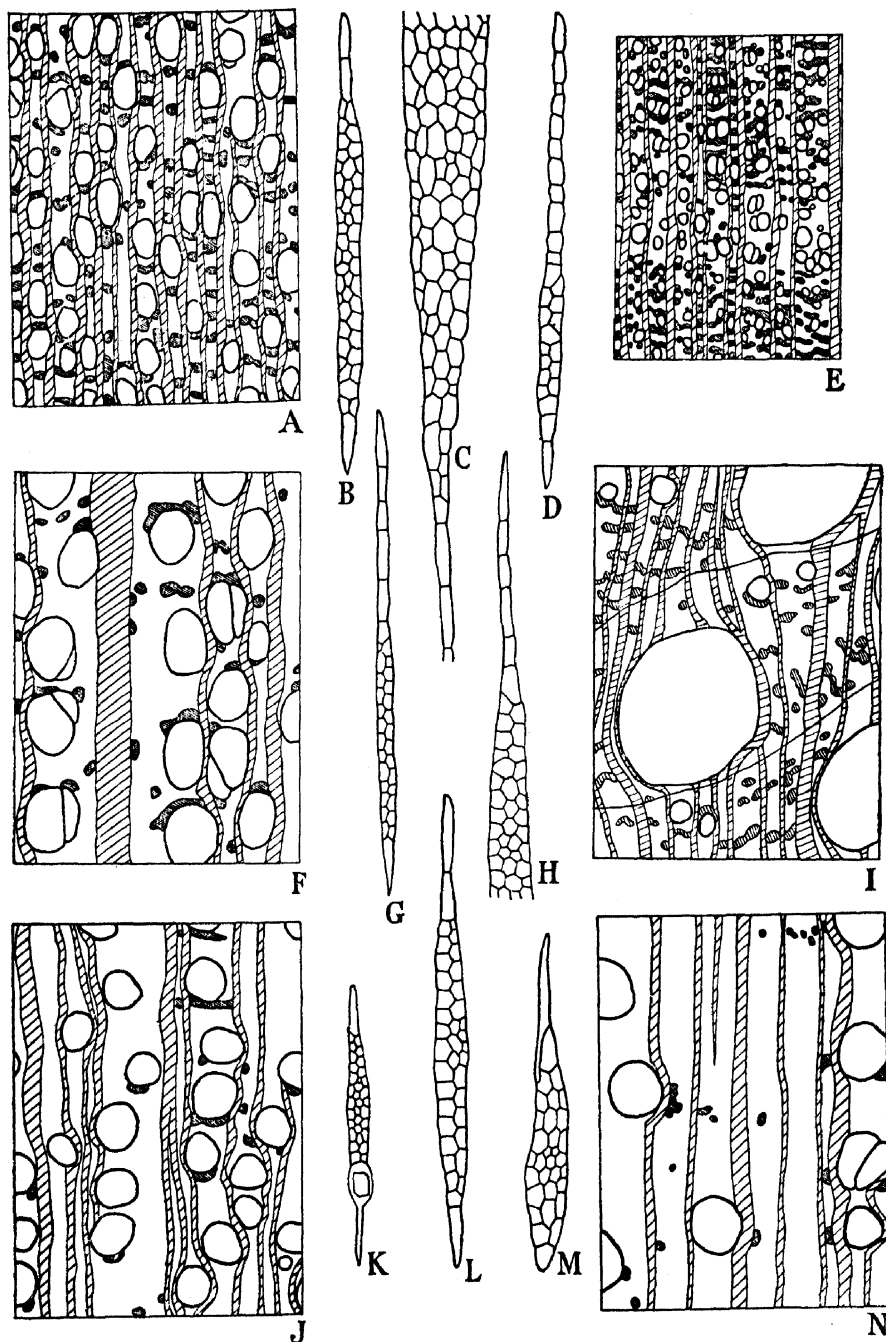


FIG. 45. **THEACEAE**, A–G, K–L, and N; **ACTINIDIACEAE**, H–I; **BONNETIACEAE**, J and M
A, *Adinandra villosa* Choisy. B, *Gordonia concentricatrix* Burk. C, *Anneslea crassipes* Hook. f.
D, *Freziera* sp. E, *Camellia japonica* Linn. F, *Ternstroemia penangiana* Choisy. G, *Schima wallichii*
Choisy. H, *Actinidia callosa* Lindl. I, *A. callosa* Lindl. J, *Bonnetia crassa* Gleason. K, *Camellia*
japonica Linn. L, *Ploiarium* sp. M, *Bonnetia crassa* Gleason. N, *Ploiarium* sp.

in number even within single genera, mostly 30–140 per sq. mm., fewest (16–40) in some species of *Adinandra*, *Gordonia*, *Schima*, and *Ternstroemia*, more than 100 per sq. mm. in some species of *Adinandra*, *Camellia*, and *Sakakia*, exceptionally numerous in some species of *Camellia*, up to 250 observed by the author and up to 400 reported by Kanehira (1206); semi-ring-porous in some species of *Camellia*, *Laplacea*, and *Pyrenaria*; spiral thickening present in *Adinandra*, *Camellia*, *Eurya*, *Franklinia* (1861), *Gordonia* (1861), *Sakakia*, *Schima*, *Stewartia*, and *Ternstroemia*, the spirals sometimes limited to the tips of the elements and sometimes surrounding and linking together the pit borders, e.g. in *Camellia*. Perforation plates very oblique, scalariform and often with numerous bars (up to 100). Intervascular pitting often difficult to observe owing to the absence of vessel groups, typically scalariform to opposite, distinctly opposite in *Adinandra*, *Anneslea*, *Cleyera*, *Eurya*, *Sakakia*, and *Ternstroemia*; pits to ray cells similar to the intervascular pitting in the above genera with opposite pitting, elongated, scalariform; with wide apertures and narrow borders or simple in the other genera. Occasionally with solid contents or a few tyloses. Mean member length 1.0–1.6 mm., but about 0.7–1 in *Camellia* and up to 2.4 in *Adinandra*. **Parenchyma** predominantly apotracheal, diffuse, occasionally in short tangential lines (Fig. 45 A and E); occasional narrow sheaths of paratracheal parenchyma also present in some genera (Fig. 45 F). Crystalliferous strands of chambered parenchyma and strands of barrel-shaped crystalliferous cells commonly present in *Schima*. **Rays** sometimes of two distinct widths; the larger rays most commonly 2–3 cells wide, but 4–8 cells wide in some species of *Anneslea*, *Camellia*, *Eurya*, *Gordonia*, *Pyrenaria* (1154), and *Ternstroemia*; almost exclusively uniseriate in some species of *Adinandra* and *Schima*, e.g. *A. dumosa* Jack. and *S. noronhae* Reinw., and also, according to Record (1861), in *Franklinia* and *Gordonia lasianthus* Linn.; multiseriate rays usually less than 1 mm. high, but over 2 mm. and often very high in *Adinandra*, *Anneslea*, *Cleyera*, *Eurya*, and *Ternstroemia*; uniseriate rays of multiseriate species composed of upright cells only, varying from moderately numerous and high, to few and low, e.g. in *Camellia* and *Stewartia*; 9–17 rays per mm.; heterogeneous (mostly Kribs's Types I and II A), typically with uniseriate marginal rows of 4–10 upright cells, but with only 2 or 3 rows in *Camellia* and *Stewartia*; sheath cells common in *Ternstroemia* and, according to Janssonius (1154), occasionally present in *Camellia*, *Eurya*, and *Ternstroemia*. Swollen ray cells containing solitary crystals present in *Camellia* (Fig. 45 K) and, according to Vestal (2329), druse crystals present in *Camellia*, *Gordonia*, and *Schima*. **Fibres** with conspicuous bordered pits (smaller in *Stewartia*) on all walls, sometimes more numerous on either the radial or the tangential walls (Janssonius 1154); walls often very thick. Mean length 1.2–3.1 mm., up to 2 mm. or more in some species of *Adinandra*, *Cleyera*, *Eurya*, *Gordonia*, and *Schima*.

ROOT

Root most fully examined by Beauvise (163) in *Camellia sasanqua* Thunb. where it is characterized by a rapidly caducous piliferous layer; a cortex of about 12 layers of parenchyma; a slightly suberized endodermis; a central cylinder containing 2 groups of xylem and 2 of phloem. Structure very similar in *Eurya* sp.

ANOMALOUS GENERA

The anatomy of the following genera has been described separately because their taxonomic position is rather uncertain.

I. CLEMATOCLETHRA Maxim.

Chinese shrubs. Description based on Beauvisage's (163) account of *C. scandens* (Franch.) Maxim.

LEAF

Mesophyll consisting of 2 layers of palisade tissue, together with very lacunar spongy tissue. Arm-palisade cells present. Large, multicellular and uniseriate **hairs** occur on the petiole. **Petiole**, in transverse sections, exhibiting a U-shaped vascular strand with outwardly directed arms in *C. scandens*, but vascular strands tending to form a closed ring in *C. tiliacea* Kom. **Mesophyll** containing **raphides** situated in elongated tubes or sacs; similar crystals also present in the phloem of the veins. Raphides sometimes replaced by crystal-sand.

AXIS

YOUNG STEM

Cork arising superficially; consisting of about 5 layers of cells with thin walls. **Pericycle** generally provided with a composite, continuous ring of sclerenchyma, although isolated groups of fibres also recorded. **Xylem** with isolated, infrequent vessels, 50–70 μ in radial diameter, and numerous, narrow medullary rays. **Pith** becoming hollow. **Raphides** recorded in cortex and in the phloem.

II. SLADENIA Kurz.

Shrubs from the Himalayan region belonging to the single species *S. celastriifolia* Kurz. the following description is based on that of Beauvisage (163).

LEAF

Dorsiventral. **Mesophyll** consisting of a single layer of tall palisade cells, and very lacunar spongy parenchyma. **Stomata** confined to the lower surface; ranunculaceous. Large clustered **crystals** present, particularly in the petiole. Vascular system of the **petiole** appearing, in transverse sections, as a single U-shaped strand.

AXIS

YOUNG STEM

Cork originating in the epidermis. **Pericycle** containing isolated groups of fibres when young, but becoming converted to a continuous composite ring; the latter stated to consist of 3–4 layers of cells. **Phloem** containing stone cells, either solitary or in groups; often accompanied by solitary crystals in the adjoining cells. **Xylem** with vessels in radial rows; the latter 35–65 μ in diameter; provided with bordered pits and scalariform perforation plates. Wood fibres in radial rows, elements with wide lumina. Rays 1–2 cells wide. **Pith** consisting of thickened pitted cells. Clustered **crystals** present in the cortex, often arranged in axial rows. Raphides and crystal-sand absent.

III. TREMATANTHERA F. von Müll.

Shrubs belonging to the single species *T. dufauri* F. von M. The following description is based on Beauvisage's (163) account.

LEAF

Dorsiventral. A single layer of aqueous **hypoderm** present. **Mesophyll** consisting of 3 layers of palisade tissue interspersed with cells containing **raphides**, and a broad region of lacunar spongy tissue. Vascular system of the **petiole** appearing, in transverse sections, in the form of a closed ring surrounding an accessory, collateral bundle. Two accessory bundles also present in the cortical region of the petiole.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis. Outer part of the **cortex** containing chlorophyll; middle part collenchymatous, but containing isolated or small groups of sclereids; inner part consisting of thin-walled parenchyma. **Endodermis** consisting of broad cells containing starch. **Pericycle** with a composite ring of sclerenchyma. **Xylem** containing mostly isolated vessels, each surrounded by a sheath of vasicentric parenchyma. Rays numerous, 1-2 cells wide. **Pith** sclerenchymatous in the perimedullary region; the remainder consisting of cells of very unequal sizes. Elongated cells containing **raphides** and other forms of crystals also occur in the middle and inner part of the cortex.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The genera placed by Bentham and Hooker in the Ternstroemiaceae do not constitute a homogeneous group. This was fully appreciated by Solereder who was unable to find any anatomical characters which are common to all of them. The genera here described under Theaceae are fewer in number, and approximate to those regarded as members of this family by Melchior (1481). *Bonnetia* and *Pelliciera* have also been excluded and described under separate families. From a perusal of the account of the anatomical structure of the genera described above (excluding those which are anomalous), it is clear that they constitute a far more homogeneous group than those in the Ternstroemiaceae of Bentham and Hooker. It is interesting to note, however, that certain species of *Freziera* differ from the rest of the family in having, in the petiole, a solitary vascular strand which appears as a closed ring in sections through the distal end. *Archytæa* differs from the other genera in having decurrent leaf bases, and rubiaceous stomata. *Stewartia* appears also to be somewhat aberrant in the absence of idioblasts from the leaf. The most noteworthy variation in stem structure is between those genera in which the phellogen arises in the sub-epidermis and those in which its origin is pericyclic. It is doubtful, however, whether much significance should be attached to this variation, because similar divergences are known to occur within other

families. The tribes Camellieae and Ternstroemieae do not appear to be very clearly demarcated on anatomical grounds.

The taxonomic position of the genera described above as anomalous has never been well established, since they possess characters in common with the Dilleniaceae and Theaceae. In this connexion it is interesting to note that Hutchinson (1113) has pointed out the probable existence of affinities between the Dilleniales and Theales. *Sladenia* seems to differ somewhat from most of the Dilleniaceae, notably in the absence of raphides, and in the distribution of the vessels in radial groups.

(ii) FROM WOOD STRUCTURE

Excluding *Asteropeia*, *Bonnetia*, *Tetramerista* and possibly *Ploiarum*, leaves genera within the family that are much more uniform in structure.

ECONOMIC USES

Camellias are cultivated in gardens as ornamental shrubs. The roots and bark have sometimes been used as a source of tannin. Tea consists of the dried tips and upper leaflets of *Camellia sinensis* (L.) O. Ktze. The microscopical characters of tea include the following. Upper epidermis consisting of cells $50\ \mu$ in diameter with slightly sinuous anticlinal walls, devoid of stomata or hairs. Lower epidermis consisting of cells about $70\ \mu$ in diameter with more sinuous anticlinal walls. Stomata confined to the lower surface, surrounded by 3-4 narrow, subsidiary cells. Amount and distribution of cutin in the guard cells as seen in transverse section believed by Rehfoos (1905) to be of diagnostic value in the recognition of different varieties of tea, and also as a means for distinguishing 'Camellia' from tea-leaves. Palisade cells circular in surface view. Spongy parenchyma consisting of star-shaped cells. Idioblasts in the mesophyll very variable in form and size, up to $150\ \mu$ long, broadened at the ends and provided with simple or forked branches. Rosette crystals abundant. Vascular bundles and idioblasts in tea-leaves are coloured pink when treated with strong hydrochloric acid owing to the presence of phloroglucin. Stracke (2211) claims to have shown that this reaction is not given by substitutes for tea such as *Camellia japonica* Linn. Recent investigations into the structure and physiology of the tea plant have been made by Bond (227, 228).

The timbers of this family, which are of the general utility class, are not much used. Campano, *Laplacea brenesii* Standl., however, is reported (1886) to be 'one of the best known local timbers on the market in the Cartago region of Costa Rica'. Pearson and Brown (1679) include Needle Wood, *Schima wallichii* Choisy, among the commercial timbers of India.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Adinandra, Anneslea, Archytaea, Camellia,* Clematoclethra, Cleyera,* Eurya,* Franklinia, Freziera, Gordonia, Laplacea, Nabiasodendron, Ploiarum, Pyrenaria, Schima, Sladenia, Stewartia,* Ternstroemia, Ternstroemiopsis, Trematanthera, Tutcheria,* Visnea.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Adinandra, Anneslea, Camellia, Cleyera, Eurya, (Franklinia), Gordonia, Haemocharis, Laplacea, Pyrenaria, Sakakia, Schima, Stewartia, Ternstroemia.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Bond, T. E. T. 227, 228, Foster 694, Heilbronn 932, Hutchinson 1113, Kobuski 1259, Lepeschkin 1361, Melchior 1481, Pekelharing 1681, Rehfoos 1905, Stracke 2211.

(ii) *On Wood Structure*

Beekman 167, den Berger 179, 182, Janssonius 1154, Kanehira 1206, 1209, Pearson and Brown 1679, Record 1743, 1843, 1851, 1861, 1864, Record and Hess 1886, Tang 2231, Vestal 2329, Williams 2430, Yamabayashi 2478.

51. ACTINIDIACEAE

(FIG. 45 on p. 186; FIG. 46 on p. 192)

SUMMARY

Trailing and climbing shrubs from the Far East belonging to the single genus *Actinidia*. The most significant anatomical character is the occurrence of raphides. The wood exhibits the following characters. **Vessels** small or of two types, small and large; with spiral thickening; perforation plates simple or scalariform; members moderately short. **Parenchyma** apotracheal, diffuse or in irregular bands. **Rays** up to 6 cells wide, markedly heterogeneous. **Fibres** with bordered pits.

LEAF

Dorsiventral. **Hairs** including simple, uniseriate, and multicellular glandular types. **Stomata** confined to the lower surface; ranunculaceous. **Mesophyll**. Palisade tissue in *A. callosa* Lindl. consisting of one layer. Arm palisade cells stated sometimes to occur. Spongy parenchyma in the same species with abundant intercellular spaces. **Petiole**, in transverse sections through the distal end, exhibiting a crescentic strand with incurved ends in *A. kolomikta* Maxim. and a dorsally flattened almost or completely cylindrical strand in *A. callosa* Lindl. (Fig. 46 c); accessory strands present in the wings in both species. **Raphides** present in elongated sacs or tubes, situated in the mesophyll and also in the cortical region of the petiole.

AXIS

YOUNG STEM (Fig. 46 j)

Cork arising superficially at an early stage; consisting of thin-walled cells with brown contents. Later formed cork relatively deep-seated in origin. **Pericycle** containing a continuous but very narrow ring of sclerenchyma. **Phloem** devoid of sclerenchymatous elements. **Xylem** with relatively infrequent, mostly solitary vessels, the latter varying in diameter in different species. Vessels of the primary xylem tending to be in radial rows. Perforation plates mostly scalariform, with numerous bars, but simple perforations also occur. Wood fibres in radial rows separated by narrow medullary rays.

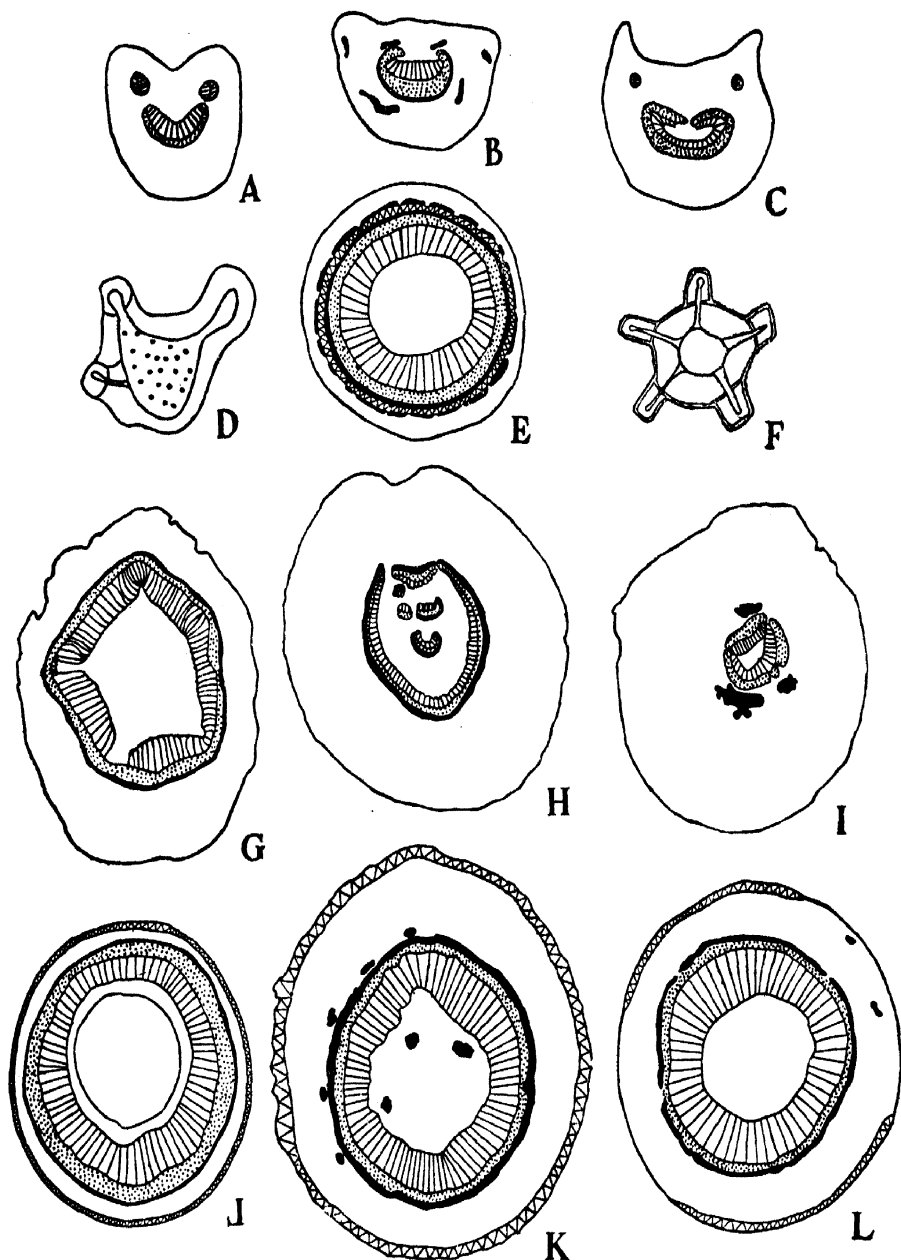


FIG. 46. *STACHYURACEAE*, A; *THEACEAE*, B, D-F, and L; *ACTINIDIACEAE*, C and J; *BONNETIACEAE*, G; *SAURAUACEAE*, H; *MARCGRAVIACEAE*, I and K

A, *Stachyurus chinensis* Franch. Petiole $\times 15$. B, *Camellia cuspidata* Veitch. Petiole $\times 15$. C, *Actinidia callosa* Lindl. Petiole $\times 15$. D, *Cleyera ochracea* DC. Idioblast from cortex $\times 300$. E, *Camellia cuspidata* Veitch. Stem $\times 15$. F, *Cleyera ochracea* DC. Idioblast from cortex $\times 300$. G, *Bonnetia anceps* Mart. et Zucc. Stem $\times 5$. H, *Saurauia subspinoso* Anthony. Petiole $\times 10$. I, *Marcgravia umbellata* Linn. Petiole $\times 13$. J, *Actinidia callosa* Lindl. Stem $\times 12$. K, *Marcgravia umbellata* Linn. Stem $\times 13$. L, *Cleyera ochracea* DC. Stem $\times 15$.

Pith septate in *A. kolomikta* Maxim. becoming hollow in *A. callosa* Lindl. Very long **raphides**, situated in elongated idioblasts or sacs, present in the primary cortex, phloem, and pith. These crystals sometimes resemble a gummy or resinous material on superficial examination, possibly owing to the presence of mucilage. The true nature of the crystals is most clearly revealed in longitudinal sections. Crystals exhibiting forms transitional between raphides and crystal-sand also occur, particularly in the phloem.

WOOD (Fig. 45 H-I)

Vessels generally of two types, (a) large, tending to be 'locally zonate' (533), and with simple perforations, and (b) small, mostly solitary and with simple or scalariform perforation plates, the latter with several to many bars; with spiral thickening. With only small vessels in the material examined of *A. kolomikta* Maxim. Intervascular pitting small, often with coalescent apertures; pits to ray and wood parenchyma similar. Mean member length 0.7-0.8 mm. **Parenchyma** apotracheal, scattered and in irregular lines (Fig. 45 I). Strands commonly of 8 cells. **Rays** tending to be of two sizes, uniseriate and composed entirely of square or upright cells, or multiseriate, up to 6 cells wide, composed of procumbent cells with several marginal rows of square or upright cells (Kribs's Heterogeneous Type I). **Fibres** with numerous, distinctly bordered pits on both radial and tangential walls.

ROOT

Raphides present.

TAXONOMIC NOTES

Actinidia probably has affinities with the Dilleniaceae and Theaceae.

GENUS DESCRIBED

Actinidia.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Cr  t   498, Gilg and Werdemann 782.

(ii) *On Wood Structure*

den Berger 182, Dadswell and Record 533, Record 1843, 1851, Vestal 2329.

52. BONNETIACEAE

(FIG. 45 on p. 186; FIG. 46 on p. 192)

SUMMARY

Bonnetia, which is a Brazilian genus, has the general features of the Theaceae but the leaf bases are decurrent, whilst the **stomata** are rubiaceous. The wood exhibits the following characters. **Vessels** solitary, perforations simple, intervacular pitting alternate, pits to ray cells large, members of medium length to moderately short. **Parenchyma** varying from predominantly diffuse to predominantly paratracheal (aliform). **Rays** up to 2 or 3 cells wide, with numerous uniseriates, heterogeneous. **Fibres** with

conspicuous bordered pits on all walls, of medium length to moderately short. Vasicentric **tracheids** present.

LEAF

Lamina thick, dorsiventral; the upper surface covered with a thick smooth cuticle. Cells of the **epidermis** of two very distinct sizes, the larger ones being very tall and filled with a mucilaginous secretion. The size and arrangement of the mucilaginous cells vary in different species, and in some the cells appear to form a hypoderm. **Stomata** confined to the lower surface; rubiaceous. **Mesophyll** consisting of 2–5 layers of short palisade cells, and a broader region of spongy tissue. **Midrib** containing an annular vascular strand, surrounded by a sclerified pericycle; usually including some mucilaginous cells on the lower side. **Petiole**, in transverse sections, exhibiting a median vascular strand which is usually crescent-shaped or almost cylindrical through the ends being strongly incurved. In some sections of *B. anceps* Mart. it was completely closed. The median vascular strand is accompanied on either side by a few small bundles.

AXIS

YOUNG STEM (Fig. 46 G)

Epidermis covered with a thick, smooth cuticle. **Cork** superficial. **Cortex** somewhat spongy; containing a few unbranched, thick-walled, sclerenchymatous idioblasts and also cluster crystals. **Pericycle** including a composite, continuous, or slightly interrupted ring of sclerenchyma. **Phloem** and **xylem** in the form of continuous cylinders traversed by narrow rays. Strands of fibres noted in the phloem of *B. anceps* Mart. Vessels of *B. anceps* mostly isolated, except in the primary xylem where they are in radial rows and more oval in shape, up to about 90 μ in radial diameter; perforations not easily seen, but simple and scalariform types with few bars apparently present. (See also 'Wood'.) Wood fibres in the same species provided with abundant bordered pits. Perimedullary region composed of a narrow zone of lignified elements. **Pith** spongy, composed of somewhat elongated, sclerosed, pitted cells and usually containing cluster crystals. **Crystals**, see 'Cortex' and 'Pith' above.

WOOD (Fig. 45 J and M)

Vessels moderately small (mean tangential diameter 50–100 μ) to medium-sized (100–200 μ); exclusively solitary; 9–25 per sq. mm. Perforations simple, slightly oblique (see also 'Young Stem'). Intervascular pitting alternate, moderately large, sometimes tending to be scalariform near the primary wood; pits to ray and wood parenchyma commonly large and almost simple. Solid deposits and tyloses sometimes abundant. Mean member length 0.3–0.8 mm. **Parenchyma** varying from predominantly paratracheal with a little diffuse to predominantly diffuse, with a few cells associated with the vessels; the paratracheal parenchyma commonly as small aliform clusters of cells at the sides of the vessels; sometimes, e.g. in *Bonnetia tristyla* Gleason, tending to surround the vessels except on the abaxial sides (Fig. 45 J). Sometimes containing chambered crystals. Strands commonly of 2–4 cells. **Rays** up to 2 or 3 cells wide; less than 1 mm. high; uniseriates numerous, composed of high

upright cells and commonly only 1 or 2 cells high; 8-12 rays per mm.; distinctly heterogeneous (Kribs's Type II A), usually with 1-4 marginal rows of square to upright cells, but with more in some species. Solid contents abundant. **Fibres** with very numerous, conspicuous bordered pits on both radial and tangential walls. Walls very thick. Mean length 0.8-1.1 mm. **Vasicentric tracheids** present.

TAXONOMIC NOTES

Bonnetia possesses characters in common with the Theaceae, although it differs from that family in a few respects. It seems to be a matter of opinion whether the genus should be placed in a distinct family, or regarded as a tribe or sub-family within the Theaceae.

Vestal (2329) considers that the anatomical evidence supports the suggestion that this group stands as a connecting-link between the Theaceae and the Guttiferae.

There is a very close resemblance between the wood anatomy of some species of *Bonnetia*, e.g. *B. tristyla* Gleason, and some members of the Kielmeyeroideae, e.g. *Caraipa richardiana* Camb., the points of difference being mainly the exclusively uniseriate rays of the latter and the occurrence of the parenchyma (otherwise similar) on the abaxial and not on the axial sides of the vessels.

GENUS DESCRIBED

(i) FOR GENERAL ANATOMY

B. anceps Mart.,* *B. roraimae* Oliv.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Bonnetia.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163.

(ii) *On Wood Structure*

Record 1861, Record and Hess 1886, Vestal 2329, Williams 2430.

53. CARYOCARACEAE

(FIG. 47 on p. 202)

SUMMARY

A family of trees and shrubs from Latin American countries, comprising the two genera *Anthodiscus* and *Caryocar*. The wood exhibits the following characters. **Vessels** moderately small in *Anthodiscus*, large in *Caryocar*; perforations simple; intervacular pitting alternate, medium-sized and with large simple pits to ray cells in *Caryocar*, minute and with pits to ray cells similar in *Anthodiscus*; members of medium length to moderately long. **Parenchyma** predominantly apotracheal (diffuse) but with some paratracheal in *Caryocar*, paratracheal only (vasicentric to slightly aliform) in *Anthodiscus*; crystal druses sometimes present. **Rays** with small biseriate parts and numerous marginal

rows of square to upright cells; druse crystals sometimes present. **Fibres** with simple pits; occasionally septate in *Caryocar*, of medium length to moderately long. **Anomalous structure** has been recorded in the root of a *Caryocar*.

LEAF

Generally dorsiventral, but sometimes tending to be centric, e.g. in *Caryocar glabrum* Pers. and certain other species of *Caryocar*. **Hairs** infrequent or absent; short, bent, pointed, unicellular trichomes recorded on the petiole of *Anthodiscus*. **Extra-floral-nectaries** present at the margin of the young leaf and on the stipules. Paired **hydathodes** also present near the apices of the stipules. **Cork warts** recorded on the lower surface of *Caryocar*. **Cuticle** on both surfaces thick. **Stomata** mostly confined to the lower surface, but a few in depressions beside the veins on the upper surface in *Caryocar nuciferum* Linn. observed by Blank (203), who also counted up to 435 per sq. mm. on the lower surface. Stomata ranunculaceous in *Caryocar*. A single layer of aqueous **hypoderm** recorded in *Anthodiscus*. **Mesophyll** including 2 layers of palisade cells in *Caryocar nuciferum* according to Blank (203); spongy portion with but few intercellular spaces in the same species. Branched, sclerenchymatous idioblasts present in the mesophyll (in *C. nuciferum* especially beside the veins and at the leaf margin) and also in the ground tissue of the petiole in both *Anthodiscus* and *Caryocar*. Vascular bundles of the **veins** accompanied above and below but not surrounded by strands of cellulose fibres in *C. nuciferum*. Vascular structure of the **midrib** of *Caryocar* similar to that of the petiole (see below). **Petiole** in *Caryocar* sometimes becoming covered with 2-4 layers of cork. Petiolar vascular system in *Caryocar* described by Blank (203) as consisting of bundles which unite at the distal end to form a sinuous ring, the latter being accompanied by a few cortical and more numerous (up to 10 in *C. brasiliensis* St. Hil.) medullary strands. Petiolar vascular strands said to be separate at the base and at the distal end, but united to form a cylinder in the middle portion of the petiole in *Anthodiscus*. **Crystals** numerous in the palisade tissue of *Caryocar nuciferum*. Prismatic crystals also recorded in the petiolar ground tissue of *Anthodiscus*. Dark spots in the lamina of *Caryocar nuciferum*, visible by transmitted light, represent **tanniferous cells**, according to Blank (203).

AXIS

YOUNG STEM

Surface in *Caryocar* said to be covered with abundant short **hairs** when very young, but these soon become detached. **Cork** arising in the sub-epidermis or outer part of the cortex; consisting, in *Caryocar*, of a mixture of cells with thin walls and others with U-shaped thickenings. Primary **cortex** about 10 cells wide; including nodular, sclerenchymatous idioblasts. **Endodermis** in *Caryocar nuciferum* Linn. said by Blank (203) to be clearly defined but to be devoid of caspary thickenings. **Pericycle** in *Caryocar* bounded externally by a ring of fibres locally interrupted by parenchymatous cells. **Phloem** and **xylem** in the form of continuous cylinders traversed by narrow rays. Occasional fibres present in the phloem. Vessels tending to be in radial multiples of 2-3 in *Caryocar*; generally solitary in *Anthodiscus*; up to 60 μ in

radial diameter in *Anthodiscus*, rather larger in *Caryocar*; perforations transverse to very oblique in both genera but always simple. **Pith** in *Anthodiscus* sclerified and containing rounded, sclerenchymatous idioblasts. Only the peripheral part of the pith in *Caryocar* lignified when young, but becoming more completely lignified when older, or with the central portion of the pith sometimes becoming disorganized. Branched, sclerenchymatous idioblasts present in the pith of the same genus. Knee-shaped **crystals** and less numerous druses accompany the pericyclic sclerenchyma of *Caryocar* according to Blank (203); cluster crystals also recorded in the secondary phloem. **Secretory canals** observed by Blank (203) in the hypocotyl and base of the stem of *Caryocar nuciferum*.

WOOD

Caryocar (Fig. 47 E and G)

Vessels medium-sized (mean tangential diameter 100–200 μ) to large (more than 200 μ); solitary and in radial multiples of 2 or 3 cells; 1–2 per sq. mm. Perforations typically simple, but Williams (2429, 2430) notes a tendency to multiple plates. Intervascular pitting alternate, moderately large; pits to ray cells often large, irregularly elongated and simple. Tyloses present and often abundant. Mean member length about 0.8 mm. (Kribs 1283, Vestal 2329). **Parenchyma** predominantly apotracheal, as scattered cells and short tangential lines, but with some paratracheal parenchyma (vasicentric to slightly aliform) in addition (Fig. 47 G). Chambered cells containing solitary crystals moderately common, sometimes containing druses (2329). Strands commonly of 8 cells. **Rays** up to 2 cells wide and often more than 1 mm. high; the biseriate parts seldom more than 7 cells high, little wider than the uniseriate cells and often more than one per ray (Fig. 47 E); uniseriates not very common (most of the rays being biseriate in part), composed entirely of square to upright cells; 11–18 rays per mm.; markedly heterogeneous (Kribs's Type II A), with several marginal rows of square to upright cells. Crystals sometimes present in subdivided marginal cells and sometimes consisting of druses (2329). **Fibres** with small simple pits, mostly on the radial walls. Septa rare to common (Williams 2429). Walls very thick and often with a gelatinous inner layer. Mean fibre length about 1.8–2.0 mm. (Kribs 1283, Williams 2430).

Anthodiscus (Fig. 47 F and H)

Vessels moderately small (mean tangential diameter 50–100 μ), solitary and in short radial multiples of 2 or 3 cells; about 15 per sq. mm. Perforations typically simple, but Vestal (2329) refers to occasional scalariform plates. Intervascular pitting alternate, minute; pits to ray cells similar. Solid deposits common; tyloses absent. Member length about 0.7 mm. **Parenchyma** paratracheal, partially surrounding the vessels and sometimes slightly aliform (Fig. 47 H). Chambered cells containing crystals present in some species, but apparently absent from others (1886). Strands commonly of up to 6–8 cells. **Rays** similar to those of *Caryocar* except for the presence of abundant gum-like deposits and the absence of crystals. **Fibres** similar to those of *Caryocar* except that gelatinous layers and septa are absent, mean length about 1.5 mm.

ANOMALOUS STRUCTURE, *see* 'Root' below

ROOT

The root structure of *Caryocar nuciferum* Linn. has recently been investigated by Blank (203) from whose account the following particulars are taken.

(i) ADVENTITIOUS AND SUBSIDIARY ROOTS

Most of the cells of the sub-epidermal layer provided with strongly thickened and suberized inner tangential walls, but occasional unthickened cells also present. **Endodermis** also suberized, but casparian thickenings visible only when young. Primary **vascular structure** diarch. **Phloem** well developed when roots are sufficiently mature. Paired, monoclinic **crystals** of calcium oxalate present.

(ii) PRINCIPAL ROOTS ARISING FROM THE SWOLLEN BASE OF THE HYPOCOTYL

Several layers of cells with suberized walls and tanniniferous contents present in the hypodermal region. **Endodermis** with conspicuous casparian thickenings. Primary vascular structure triarch, tetrarch, pentarch, hexarch, or octarch. **Phloem** including fibres. **Xylem** with more numerous vessels than in the adventitious and subsidiary roots. Wood fibres with lignified primary and unlignified secondary walls. Medullary rays mostly 2-6 cells wide. **Anomalous structure.** Xylem and phloem of the normal ring show unequal development at different points on their circumference. A second xylem body, devoid of vessels, develops in the large pith, partly by lignification of the pith cells and partly from 2 to 6 small groups of meristematic cells. The latter cut off xylem on the outside and phloem on the inside, but the phloem becomes surrounded by xylem and is thus interxylary. The interxylary phloem ends blindly in the tuberous base of the hypocotyl at one end and towards the root apex at the other. This anomalous structure is of the *corpus lignosum foraminulatum* type. More towards the apex of the root, cork cells are differentiated from the abnormal phloem tissue, and a phellogen may also arise between them and the phloem. The abnormal xylem locally traverses the almost closed inner phloem ring and so unites with the inner ring of cork. All of the abnormal cork cells contain tannin, or their end walls sometimes break down to form larger tanniniferous cavities. **Secretory cavities** present in the normal protophloem in the portion of the root nearest to the swollen base of the hypocotyl. Knee-shaped **crystals** present in both the normal and the abnormal phloem.

TAXONOMIC NOTES

The presence of idioblasts, the nature of the hairy covering, and the sub-epidermal origin of the cork are suggestive of affinities between the Caryocaraceae and Theaceae. The vascular system of the petiole of the Caryocaraceae is more complex, however, and since considerable taxonomic significance can probably be attached to this difference, it seems probable that the Caryocaraceae should be regarded as a distinct family. Blank (203) believes that the secretory cavities in the root, stem base and hypocotyl of *Caryocar* are indicative of affinities with the Guttiferales.

Vestal (2329) suggests a close affinity between *Caryocar* and *Tetramerista*,

but against this must be noted marked differences in ray type, intervacular and ray-vessel pitting and fibre pits.

ECONOMIC USES

'Butter Nuts' are the fruits of *Caryocar nuciferum* Linn., the seeds of which have a high content of edible fat. The structure of the fruit and seed has been investigated in considerable detail by Blank (203).

The timbers of some species of *Caryocar* are well known locally and are used for such purposes as shipbuilding, warehouse flooring, wheel hubs, and felloes.

GENERA DESCRIBED

Anthodiscus, *Caryocar*.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Blank 203, Pilger 1721.

(ii) *On Wood Structure*

Benoist 170, Blank 203, Howard 1088, Kribs 1283, Pfeiffer, J. Ph. 1713, Record 1843, 1851, Record and Hess 1886, Vestal 2329, Williams 2429, 2430.

54. MARCGRAVIACEAE

(FIG. 46 on p. 192; FIG. 47 on p. 202)

SUMMARY

(i) GENERAL

A family of climbing shrubs, and epiphytes and occasional erect species which occur in Tropical America. The branch system of *Marcgravia* is dimorphic, consisting of (i) sterile portions which are attached to the substratum and bear two rows of leaves, and (ii) fertile, pendulous portions with spirally arranged leaves and a terminal inflorescence. The leaves of the sterile and fertile shoots respectively also differ in structure (see 'Leaf'). **Raphides** and **sclerenchymatous idioblasts** are two of the most characteristic anatomical features.

(ii) WOOD

Marcgravia and *Souroubea*

Vessels medium-sized to large, perforation plates simple or simple and scalariform with few bars, intervacular pitting alternate, pits to ray cells similar, members of medium length. **Parenchyma** paratracheal, vasicentric. **Rays** up to 10 or more cells wide, composed almost entirely of square and upright cells, containing raphides. **Fibres** septate, with small bordered pits, of medium length to moderately short.

Norantea

Vessels moderately small, multiples of 2-6 cells common, perforation plates scalariform with many fine bars, intervacular pitting opposite, pits to ray cells commonly unilaterally compound, members very long. **Parenchyma**

apotracheal, diffuse. **Rays** up to 10–12 cells wide, markedly heterogeneous, chambered crystalliferous cells common. **Fibres** with bordered pits, non-septate, sometimes with spiral thickening, very long.

LEAF

Dorsiventral. **Hairs** absent. Structures resembling **water-pores**, but of unknown physiological significance, present at the apices of the leaves. **Extra floral nectaries** and **cork warts** present on the lower surface of the leaf of certain species of *Marcgravia* and *Norantea*. Their physiological function is not definitely known, but they may serve for the secretion of resinous material. Cells of the upper **epidermis** provided with a thick cuticle. A single layer of aqueous **hypoderm** present beneath the upper epidermis. **Stomata** mostly confined to the lower surface, but also occurring in small numbers on the upper surface in *Marcgravia*. **Mesophyll** consisting of 1 or 2 layers of palisade tissue, accompanied by a broader, lacunar spongy tissue. Sclerenchymatous idioblasts present in the mesophyll, and in the cortical parenchyma of the petiole in all genera; exhibiting a variety of shapes and frequently much branched, especially in *Norantea*. **Petiole**, in transverse sections, exhibiting a single crescent-shaped vascular strand in *Marcgravia coriacea* Vahl.; a main vascular bundle in the form of an almost or completely closed ring, sometimes accompanied by a small, accessory, collateral bundle immediately external to the ring in *Marcgravia umbellata* Linn. (Fig. 46 I), *Norantea*, *Ruyschia*, *Souroubea*. **Secretory canals** present in the midrib of *Marcgravia*, and cells containing oleo-resin in the petiole of *Souroubea*.

Starch not observed in any member of the family; **inulin** thought by Melchior (1482) to be the main product of carbon assimilation at least in certain species of *Marcgravia*. Bundles of **raphides** occur in special cells in the mesophyll of *Marcgravia*, *Norantea*, *Souroubea*. Similar cells filled with mucilage or oil drops also recorded.

Leaves on the sterile differ from those on the fertile shoots in the following respects: (i) The rougher upper surface caused by the papillose epidermis. (ii) The presence of stomata on both surfaces. (iii) The absence of an aqueous hypoderm below the upper epidermis. (iv) The much greater infrequency of sclerenchymatous idioblasts in the mesophyll. (v) The chlorophyll granules being much larger than those of the fertile shoots.

AXIS

YOUNG STEM (Fig. 46 K)

Cork superficial in origin in *Marcgravia*, *Ruyschia*, *Souroubea*; cells with U-shaped thickenings in *Marcgravia*; mixed thin-walled cells and others with U-shaped thickenings or completely sclerosed in *Souroubea*. **Cortex** frequently collenchymatous in the outer part, but somewhat spongy towards the inside; sometimes including much branched sclerenchymatous idioblasts in all genera. **Pericycle** with a continuous ring of sclerenchyma, consisting of fibres when young but becoming composite when older. **Phloem** and **xylem** appearing, in transverse sections, as closed rings traversed by narrow medullary rays. Vessels in *Marcgravia umbellata* Linn. mostly somewhat angular in transverse section, up to about $45\ \mu$ in diameter; solitary or tending to be in short radial groups; lateral walls with large, circular, oval,

or horizontally elongated bordered pits with wide borders; perforations very oblique, simple. (See also under 'Wood' below.) **Pith** consisting of thin-walled cells in all genera, but with branched idioblasts interspersed amongst them in *Marcgravia*, *Norantea*, *Ruyschia*. **Raphides** present in the cortex and sometimes the pith. **Secretory cells** containing oleo-resin recorded in the cortex of *Souroubea*.

WOOD (Fig. 47 A-D)

Marcgravia and *Souroubea*¹

Vessels typically medium-sized (mean tangential diameter 100–200 μ), occasionally large (more than 200 μ) in some species of *Marcgravia* (2329); solitary and in radial pairs and threes; about 6 per sq. mm. Perforations probably typically simple in *Marcgravia*, though referred to in some of the literature (e.g. 959, 2430) as simple and scalariform; perforation plates scalariform, with few bars, in *Souroubea* and occasionally foraminose or reticulate. (See also under 'Young Stem' above.) Intervascular pitting alternate, of medium size; commonly with coalescent apertures; pits to ray cells similar, but without coalescent apertures. Mean member length about 0.6 mm. (*Marcgravia*). **Parenchyma** paratracheal, vasicentric, forming a narrow sheath 1 or 2 cells wide (Fig. 47 B). Strands commonly of 2–4 cells in *Marcgravia*. **Rays** tending to be of 2 distinct sizes, the larger up to 10 or more cells wide and several millimetres high; uniseriate numerous; both uniseriate and multiseriate rays formed predominantly of square or upright cells; about 12 rays per mm. Large cells containing raphides present in both uniseriate and multiseriate rays. **Fibres** with small bordered pits that are equally numerous on both radial and tangential walls. Septate. Walls thin to moderately thick. Sometimes with conspicuous intercellular spaces in *Marcgravia*. Mean length about 0.9 mm. (*Marcgravia*).

Norantea

Vessels moderately small (mean tangential diameter 50–100 μ); solitary and in numerous multiples of 2–6 cells; about 15 per sq. mm. Perforation plates scalariform, with many fine bars, in material examined by the author; Record and Hess (1886), however, describe the perforations as simple. Intervascular pitting opposite, of medium size; pits to ray cells similar in shape and size to the intervascular pitting, but often unilaterally compound, one elongated ray pit subtending 2–4 circular vessel pits. Mean member length about 1.7 mm. **Parenchyma** apotracheal, diffuse and in short tangential lines (Fig. 47 D). Strands mostly of 8 cells. **Rays** of 2 distinct sizes, the larger up to 10–12 cells wide and 3 mm. high; about 11 rays per mm.; uniseriate numerous, composed of high upright cells and seldom more than 1 mm. high; markedly heterogeneous (Krib's Type I), often with 10 or more marginal rows of high upright cells and with some sheath cells. Upright and procumbent cells often chambered and containing crystals. **Fibres** with rather few, large, bordered pits, which occur mostly in the radial walls. Walls rather thin. Sometimes with faint spiral thickening. Mean length about 2.5 mm.

¹ No material of *Souroubea* was examined by the author; its description here is based mainly on the data given by Hess (959) and Vestal (2329).

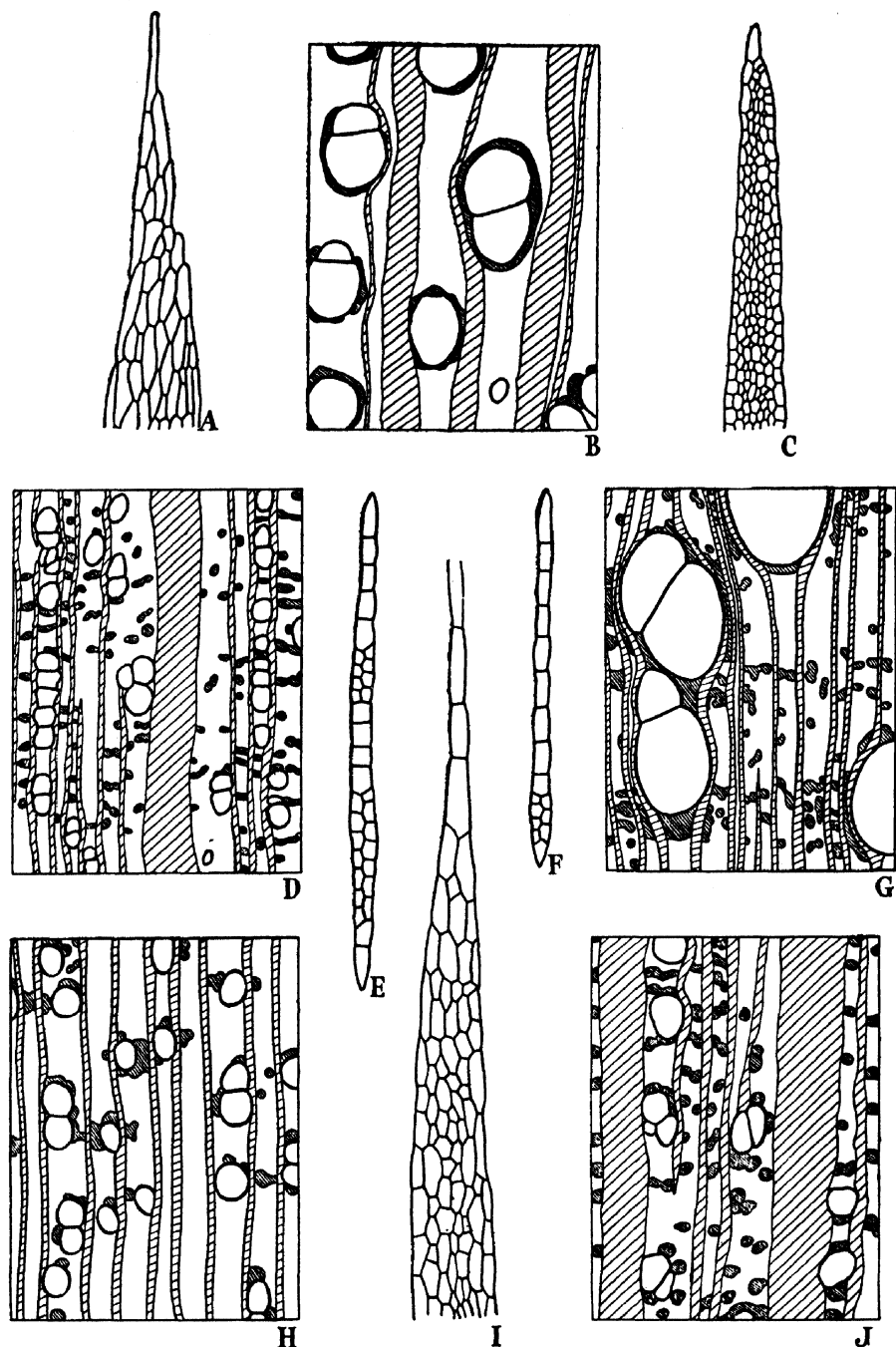


FIG. 47. MARCGRAVIACEAE, A-D; CARYOCARACEAE, E-H; SAURAUACEAE, I-J
 A, *Marcgravia rectiflora* Tr. et Pl. B, *M. rectiflora* Tr. et Pl. C, *Norantea subsessilis* Donn. D, *N. subsessilis* Donn. E, *Caryocar villosum* (Aubl.) Pers. F, *Anthodiscus trifoliatus* G.F.W. Mey. G, *Caryocar glabrum* Pers. H, *Anthodiscus trifoliatus* G.F.W. Mey. I, *Saurauia griffithii* Dyer. J, *S. griffithii* Dyer.

ROOT

Cortex containing **raphides**. **Vascular cylinder** consisting of 5 groups of xylem and 5 of phloem in *Marcgravia*.

TAXONOMIC NOTES

The anatomical characters do not sharply differentiate the Marcgraviaceae from the Theaceae, the presence of sclerenchymatous idioblasts being especially characteristic of both families. On the other hand, the more complex character of the vascular strand in the petiole, and the presence of raphides, serve to distinguish the Marcgraviaceae from the Theaceae.

Vestal (2329) considers that in the wood structure 'the genus *Norantea* possesses anatomical characters that would seem to link this family very closely to the Theaceae'.

Marcgravia and *Norantea* differ in almost every character of their wood anatomy and there appears to be no reason for associating them together. *Souroubea* appears from descriptions to be similar to *Marcgravia*. *Marcgravia* has a more highly specialized type of wood than *Norantea*.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Marcgravia,* *Norantea*, *Ruyschia*, *Souroubea*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Marcgravia, *Norantea* (*Souroubea*).

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Gilg and Werdermann 783, Melchior 1482, Richter 1933.

(ii) *On Wood Structure*

Dadswell and Record 533, Hess 959, Record 1843, 1851, Record and Hess 1886, Vestal 2329, Williams 2430.

55. MEDUSAGYNACEAE

SUMMARY

A small family from the Seychelles, consisting of shrubs belonging to the single genus *Medusagynae*. The species most fully described anatomically is *M. oppositifolia* Baker which exhibits the characters recorded below.

LEAF

Dorsiventral. **Cuticle** on the upper surface thick. Cells of the upper **epidermis** much taller than those of the lower. **Hypoderm** of 1 or 2 layers of mucilaginous cells present beneath the upper epidermis. **Stomata** confined to the lower surface; ranunculaceous. **Mesophyll** consisting of about 3 layers of palisade cells and an extensive, very lacunar, spongy mesophyll.

Vascular strand of the **midrib** in the form of a flattened ellipse, composed of numerous small vascular bundles. **Petiole**, in transverse sections, exhibiting an arc of about 6-9, variously orientated and more or less U-shaped vascular bundles. **Mucilage cells** present in the mesophyll. **Crystals** all clustered; occurring in the petiole and around the vascular strand of the midrib.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis; consisting of about 6 layers of cells, the outermost ones with thin walls, but those towards the phellogen provided with U-shaped thickenings. **Cortex** fairly broad, parenchymatous, but including a proportion of sclerosed cells and some which contain cluster crystals. Small scattered strands consisting mainly of fibres, but sometimes including a few vessels, recorded by Engler and Melchior (647) in the primary cortex. **Pericycle** containing a closed ring of sclerenchyma when very young, but the ring becomes interrupted by parenchyma and stone cells when older. **Phloem** stratified into alternating concentric rings of sieve tissue and strongly thickened cells. **Xylem** ring interrupted by primary rays which are mostly 5-8 cells wide, the secondary rays being 2-3 cells wide. Vessels mostly solitary, 15-20 μ in diameter; perforations simple. **Pith** consisting of thickened, pitted elements containing prisms of calcium oxalate. **Crystals**, see 'Cortex' and 'Pith' above.

TAXONOMIC NOTES

The taxonomic position of *Medusagyne* is somewhat uncertain, as it has been variously ascribed to the Guttiferae and Theaceae. The genus differs from the Guttiferae and Marcgraviaceae in the absence of resin-canals and from the Theaceae in the absence of the sclerenchymatous idioblasts which are a characteristic feature of the parenchymatous tissues of nearly all members of that family. It resembles the Ochnaceae in having cortical bundles.

GENUS DESCRIBED

Medusagyne.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Beauvisage 163, Engler and Melchior 647.

56. PELLICIERACEAE

SUMMARY

The sole representative of this family is *Pelliciera rhizophorae* Trian. et Planch., a tree growing in watery places in Latin American countries. In habit it resembles a *Rhizophora*. Unlike most of the true Theaceae the plant has decurrent leaf-bases. A notable anatomical feature is the occurrence of **raphides** in special cells situated in the parenchymatous tissues.

LEAF

Thick and leathery with the midrib not projecting above the surface. Dorsiventral. **Hairs.** None observed. Upper **epidermis** composed of small, polygonal cells with highly cutinized outer walls and slightly sinuous anticlinal walls. Cells of the lower epidermis somewhat larger and more thickly cutinized. **Stomata** confined to the lower surface, each surrounded by about 5 concentric subsidiary cells. A single layer of thin-walled, aqueous **hypoderm** present beneath the upper epidermis, the anticlinal walls of which become considerably contracted in herbarium material. A single layer of smaller aqueous cells also occurs on the inside of the lower epidermis. **Mesophyll** composed of 2 layers of palisade cells, interspersed with sacs of raphides, and a highly lacunar spongy tissue. Sinuous fibres, mostly lying parallel to the leaf surface, scattered throughout the mesophyll; groups of stone cells also present in the spongy tissue. **Petiole** collenchymatous in the outer part of the cortical region, but more spongy and including sinuous fibres nearer the almost annular but somewhat interrupted vascular strand; occasional raphide sacs occur in the cortical region and small prismatic crystals chiefly in the phloem.

AXIS

YOUNG STEM

Cork arising superficially in very young stems; composed of thin-walled cells. **Cortex** clearly differentiated into an outer collenchymatous and an inner spongy region. **Pericycle** bounded externally by a composite, continuous ring of sclerenchyma, with small prismatic crystals in some of the component elements. **Phloem** and **xylem** in the form of closed cylinders traversed by uniseriate rays. Vessels in radial rows of about 3-10, up to about 45 μ in radial diameter; perforations simple, oblique. Wood fibres consisting of radial rows of moderately thick-walled elements, with inconspicuously bordered pits. **Pith** consisting of spongy, parenchymatous, comparatively thin-walled but pitted cells. Branched sclerenchymatous idioblasts and elongated thick-walled fibres present in the inner, spongy portion of the cortex as well as in the pith. **Crystals**, see under 'Pericycle' above.

TAXONOMIC NOTES

Although *Pelliciera* was treated as a tribe of the Theaceae by Melchior (1481) it differs conspicuously from the other members of this family in the frequent occurrence of raphides, and in the almost annular structure of the vascular strand of the petiole. There are also other important differences in the floral and external morphological characters. Beauvisage (163), suggested that *Pelliciera* should form the basis of a family closely related to but distinct from the Theaceae, and intermediate between them and the Marcgraviaceae.

GENUS DESCRIBED

Pelliciera.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Beauvisage 163, Melchior 1481.

57. PENTAPHYLACACEAE

(FIG. 48 on p. 206)

SUMMARY

The Pentaphylacaceae are represented by the single genus *Pentaphylax*, which consists of shrubs with leathery leaves occurring in China and Malaya. The anatomical characters which have been recorded about the general anatomy refer only to *P. euryoides* G. et C. The wood exhibits the following features. **Vessels** solitary, perforation plates and intervacular pitting scalariform, members extremely long. **Parenchyma** diffuse. **Rays** up to 5 cells wide, heterogeneous. **Fibres** with distinctly bordered pits, extremely long.

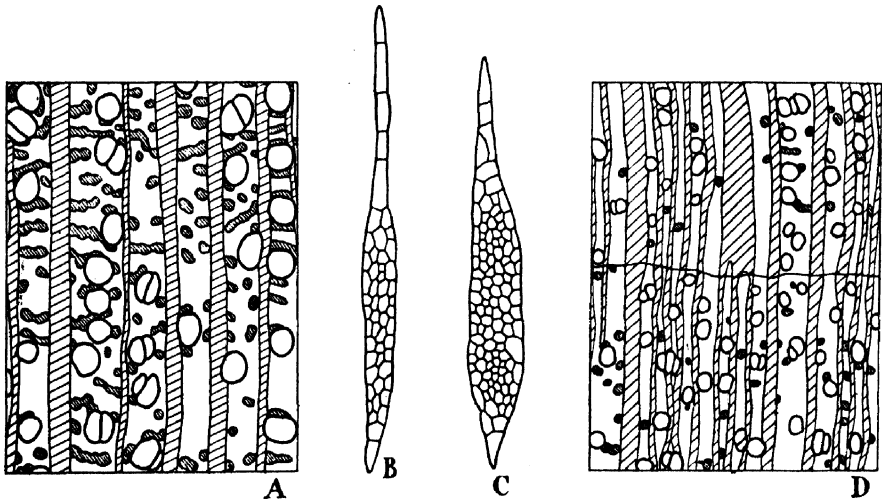


FIG. 48. PENTAPHYLACACEAE, A-B; STACHYURACEAE, C-D

A, *Pentaphylax arborea* Ridley. B, *P. arborea* Ridley. C, *Stachyurus chinensis* Franch. D, *S. praecox* S. et Z.

LEAF

Dorsiventral. **Epidermis** mucilaginous. **Stomata** confined to the lower epidermis; figured by Beauvisage (163) as rubiaceous in most instances. **Mesophyll** consisting of one layer of palisade tissue together with a region of very lacunar spongy parenchyma, the latter occupying two-thirds of the thickness of the lamina. Vascular bundles of the veins provided with a sheath of sclerenchyma. **Petiole**, in transverse sections, exhibiting a solitary, slightly U-shaped vascular strand; pericycle unglified except at the distal end. Solitary **crystals** present in the mesophyll.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis; consisting of small elements with thin walls. Primary **cortex** slightly collenchymatous in the outer part. **Endodermis** not clearly defined. **Pericycle** including a composite and continuous

ring of sclerenchyma. **Xylem** with small isolated vessels 15–30 μ in radial diameter; perforation plates scalariform; wood fibres with very thick walls; rays 1–2 cells wide, frequently contiguous to the vessels. **Pith** consisting of cells with thickened, pitted walls. **Secretory cells** with mucilaginous contents present in the cortex. Prismatic **crystals** occur in the phloem, and a solitary crystal in each cell of the endodermis.

WOOD (Fig. 48 A–B)

Vessels very small (25–50 μ mean tangential diameter) and angular; almost entirely solitary, except for apparent tangential pairs due to overlapping ends; about 30 per sq. mm. Heimsch (938) refers to spiral thickening as abundant in a twig of *Pentaphylax euroides* G. et C. but as present only in a few vessel tips in mature material of *P. arborea* Ridl. Perforation plates scalariform, usually with about 15 bars but sometimes with more than 25 (938). Intervascular pitting scalariform to transitional; pits to ray and wood parenchyma similar in outline to the intervascular pitting, but almost simple. Mean member length about 2.0 mm. **Parenchyma** apotracheal, as isolated cells scattered among the fibres, with a slight tendency to form short uniseriate lines. Strands usually of 6–8 very high cells. **Rays** up to 4 or 5 cells wide; uniseriate moderately numerous and composed of square to upright cells; about 8 rays per mm.; markedly heterogeneous (Kribs's Type I-II A), with 1–8 marginal rows of square to upright cells. Dark, gum-like deposits abundant. **Fibres** with distinctly bordered pits, which are more abundant on the radial than on the tangential walls. Walls thick. Mean length 3.3 mm.

TAXONOMIC NOTES

Pentaphylax was treated by Bentham and Hooker as a member of the Ternstroemiaceae–Ternstroemieae. It is retained in the Theaceae by Hutchinson (1113), but in the Englerian system it is treated as a separate family having affinities with the Cyrillaceae and Celastraceae. Beauvisage (163) also regards the genus as related to the Cyrillaceae. Heimsch (938) considers that, on the basis of the wood anatomy, the genus would be better placed near the Celastraceae or the Theaceae than in the Terebinthales.

GENUS DESCRIBED

(i) FOR GENERAL ANATOMY

Pentaphylax. The above description is based mainly on Beauvisage's (163) account of the structure of *P. euroides* G. et C.

(ii) FOR WOOD STRUCTURE

Pentaphylax (a single sample of *P. arborea* Ridl.).

LITERATURE

(i) On General Anatomy

Beauvisage 163, Hutchinson 1113.

(ii) On Wood Structure

Heimsch 938.

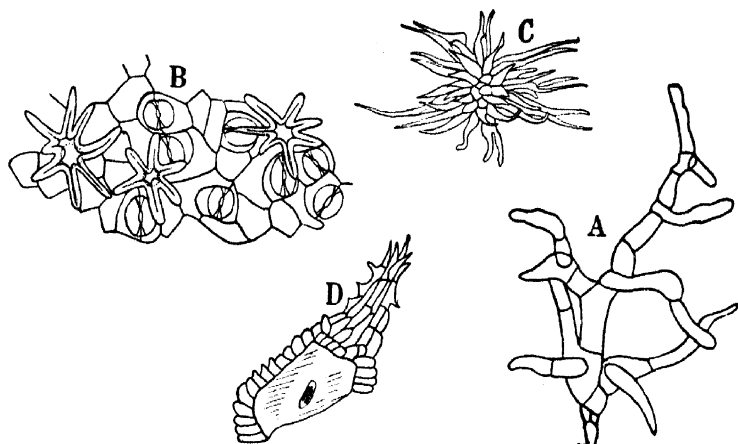


FIG. 49. SAURAUACEAE, A, C, D; GUTTIFERAE, B

A, Branched trichome of *Saurauia napaulensis* DC. B, Lower epidermis of the leaf of *Caraiþa glabrata* Mart., with stellate hairs. C, Clustered hair of *Saurauia spadicea* Bl. D, Shaggy hair of *Saurauia napaulensis* DC.—By Solereder.

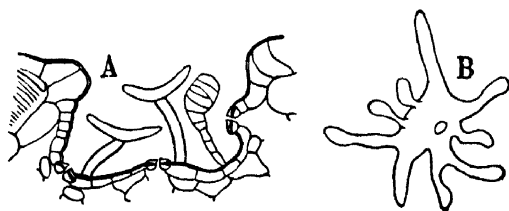


FIG. 50. CHLAENACEAE

A, Transverse section through one of the small depressions (pits) on the lower surface of the leaf of *Schizolaena rosea* Thouars. B, Small scale of *Sarcolaena multiflora* Thouars in surface-view.—By Solereder.

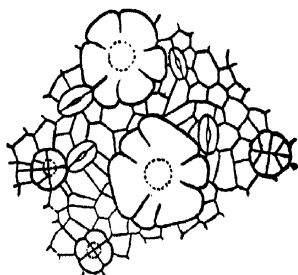


FIG. 51. DIPTEROCARPACEAE

Lower epidermis of the leaf of *Anisoptera lanceolata* Walp.—By Solereder.

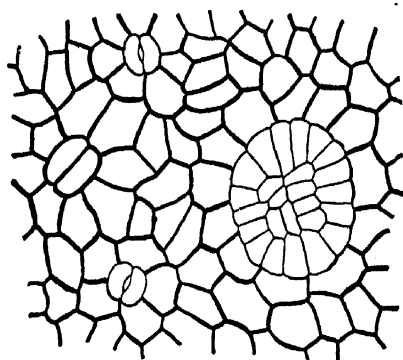


FIG. 52. ANCISTROCLADACEAE

Epidermis of lower side of leaf in *Ancistrocladus heyneanus* Wall.—By Solereder.

58. SAURAUICEAE

(FIG. 46 on p. 192; FIG. 47 on p. 202; FIG. 49 on p. 208)

SUMMARY

Trees and shrubs belonging to the single genus *Saurauia* which occurs in tropical and sub-tropical regions in Asia and America. One of the most significant anatomical characters is the occurrence of **raphides**. The wood exhibits the following characters. **Vessels** exclusively solitary, perforation plates scalariform with many bars, intervacular pitting scalariform to opposite and pits to parenchyma similar, members very long. **Parenchyma** diffuse, containing raphides. **Rays** of 2 sizes, the larger up to 6 cells wide and markedly heterogeneous. **Fibres** with distinctly bordered pits, very long.

LEAF

Dorsiventral. Clustered **hairs** (Fig. 49 c), visible to the naked eye, and branched trichomes (Fig. 49 a) present, particularly on the lower surface. Shaggy hairs (Fig. 49 d) also recorded. Two layers of **hypoderm** stated to occur beneath the upper epidermis in *S. napaulensis* DC. **Stomata** generally confined to the lower surface; some tending to be rubiaceous, but mostly ranunculaceous. **Mesophyll**. Arm-palisade cells recorded in *S. napaulensis*. **Petiole**, in transverse sections through the distal end, generally exhibiting a single U-shaped vascular strand with incurved ends, but tending to be cylindrical in certain species. About 3 medullary bundles were observed within the main U-shaped strand in *S. subspinoso* Anthony (Fig. 46 h). **Raphides** or styloids present in the spongy mesophyll and in the parenchymatous tissues and phloem of the petiole. **Secretory cells** observed in the cortical region of the petiole in *S. subspinoso*.

AXIS

YOUNG STEM

The following features were observed in *S. subspinoso* Anthony grown at Kew.

Cork arising superficially. **Pericycle** with a composite, continuous ring of sclerenchyma. **Xylem** forming a continuous cylinder, traversed by mostly narrow and occasional broader rays; including vessels with scalariform perforation plates with many bars. **Pith** broad and somewhat spongy. **Raphides** abundant, especially in elongated sacs in the phloem.

WOOD (Fig. 47 I-J)

Vessels moderately small to medium-sized (slightly smaller or larger than $100\ \mu$ mean tangential diameter); solitary, but commonly appearing as tangential pairs owing to overlapping members; angular; 8-15 per sq. mm.; spiral thickening reported (1851) on the tips of the members. Perforation plates typically scalariform, occasionally reticulate, oblique, with more than 20 and up to 50 (1154) bars. Intervacular pitting rare owing to the lack of vessel groups; when present, opposite to scalariform; pits to ray and wood parenchyma similar, often simple. Mean member length 1.5-1.8 mm.

Parenchyma apotracheal, sparse to moderately abundant, scattered and tending to form short uniseriate bands from ray to ray (Fig. 47 J); with enlarged mucilaginous cells containing raphides in some species, the crystals sometimes up to $610\ \mu$ long according to Hess (1959). **Rays** of 2 distinct sizes, the larger up to 5–10 cells wide and more than 2 mm. high; uniseriates numerous and composed entirely of high upright cells; about 13 rays per mm.; heterogeneous (Kribs's Type I), commonly with 10 or more marginal rows of upright cells; sheath cells often present; with conspicuous solid contents. Record and Hess (1886) refer to raphides as present in the rays of some species, but it seems to be more typical for raphides, when present, to occur in the parenchyma only (1959, 1154). **Fibres** with large bordered pits on both radial and tangential walls. Walls moderately thin to moderately thick. Mean length about 2.5 mm.

TAXONOMIC NOTES

Saurauia probably has affinities with the Theaceae and Dilleniaceae.

GENUS DESCRIBED

Saurauia. *†

* Represented in the Kew slide collection.

† The description of the wood was based on *Saurauia griffithii* Dyer, the only species examined by the author.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Buscallioni and Muscatello 321.

(ii) *On Wood Structure*

Hess 959, Janssonius 1154, Kanehira 1206, Record 1833, 1851, Record and Hess 1886.

59. STACHYURACEAE

(FIG. 46 on p. 192; FIG. 48 on p. 206)

SUMMARY

Shrubs or small trees belonging to the single genus *Stachyurus* which occurs in the Far East. The wood is characterized by the following features. **Vessels** small, solitary, commonly with spiral thickening, perforation plates scalariform with many bars, members very long. **Parenchyma** diffuse. **Rays** up to 2–4 cells wide, markedly heterogeneous. **Fibres** with distinctly bordered pits, sometimes with spiral thickening, long.

LEAF

Lamina dorsiventral, but with a thin mesophyll. **Stomata** confined to the lower surface; ranunculaceous. **Mesophyll**. Palisade tissue consisting of a single layer of cells in *S. praecox* Sieb. et Zucc. Spongy tissue occupying two-thirds of the thickness of the lamina. **Midrib** projecting considerably from the lower surface; supplied by a U-shaped vascular strand. **Petiole**, in transverse sections, exhibiting a large, median, arc-shaped vascular strand, accompanied by two smaller lateral ones (Fig. 46 A). No definite ring of

sclerenchyma in the pericyclic region of the petiole. Cluster **crystals** present in the spongy mesophyll and in the parenchymatous tissues of the petiole. A few of the parenchymatous cells of the petiole contain drops of an oily-looking substance.

AXIS

YOUNG STEM

Epidermis composed of dome-shaped cells with a thick cuticle. **Cork** originating in the epidermis; composed of thin-walled, tanniferous cells. **Cortex** up to about 18 cells wide; outer part composed of smaller, more compact cells than the inner part; including cells stained very darkly with haematoxylin. **Pericycle** marked by a composite, continuous ring of sclerenchyma. **Phloem** and **xylem** appearing, in transverse sections, in the form of continuous rings, interrupted only by very numerous, uniseriate rays. Vessels mostly tending to be in radial rows, but some isolated; somewhat angular in transverse section, up to about 45 μ in radial diameter (rather larger and more frequently isolated in *S. praecox* Sieb. et Zucc. than in *S. chinensis* Franch.); perforation plates scalariform, with numerous bars. Perimedullary region consisting of a narrow zone of thick-walled cells. **Pith** composed of very thin-walled parenchyma. Large cluster **crystals** present in the cortex and pith.

WOOD (Fig. 48 C-D)

Vessels very small (mean tangential diameter 25–50 μ); exclusively solitary, but commonly appearing as tangential pairs owing to overlapping members; angular; sometimes with spiral thickening (1206, 2261). Perforation plates scalariform and oblique, with about 5 bars; sometimes locally reticulate. Intervascular pitting rare, small; opposite to transitional; pits to parenchyma similar. Mean member length about 1.2 mm. **Parenchyma** apotracheal, scattered among the fibres; strands usually of 6–8 cells. **Rays** usually up to 4 cells wide, but up to 7 cells wide in *Stachyurus chinensis* Franch. and not more than 2 cells wide in *S. himalaicus* Hook. f. et Thoms. (1206); uniseriate numerous and composed entirely of upright cells; heterogeneous (Kribs's Type I), with several marginal rows of square or upright cells. **Fibres** with bordered pits on all walls; sometimes with spiral thickening, e.g. in *S. chinensis*; mean length about 1.7 mm. (1206).

TAXONOMIC NOTES

A small family of uncertain taxonomic position. It differs from most of the Theaceae in the absence of sclerenchymatous idioblasts, and by the fact that the cork arises in the epidermis. It is included by Hutchinson (1113) in the Hamamelidales, a suggestion which Tippo (2261) believes to be supported from the evidence of wood anatomy. A comparison of the stem of *Stachyurus* with those of a selection of the Hamamelidaceae certainly reveals a very strong similarity in the general topography and in some details of structure. A comparison of *Stachyurus* with some of the Flacourtiaceae indicates possible affinities with this family also. Plants which are characterized by tanniferous tissues, a somewhat spongy cortex in the young stem, xylem with small, somewhat angular vessels with scalariform perforations, and by the presence

of large cluster crystals in the parenchymatous tissues, occur in both the Flacourtiaceae and the Hamamelidaceae. In the circumstances it is difficult to decide on anatomical grounds alone to which of these families *Stachyurus* is most closely related.

GENUS DESCRIBED

Stachyurus.*†

* Represented in the Kew slide collection.

† The account of the secondary xylem is based entirely on published descriptions.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Gilg 774, Hutchinson 1113.

(ii) *On Wood Structure*

Kanehira 1206, Record 1837, 1843, 1851, Tippon 2261.

60. DIPTEROCARPACEAE

(FIG. 51 on p. 208; FIG. 53 on p. 214; FIG. 54 on p. 216; FIG. 55 on p. 218)

SUMMARY

(i) GENERAL

A family of large resinous trees, with leathery dorsiventral leaves mainly native of tropical Asia, the Monotoideae alone being African. The most outstanding anatomical characteristic is the occurrence throughout the family, except in the Monotoideae, of a branched system of **resin canals**, usually lined with a delicate epithelium. In the young stem the resin canals are always present in the pith, especially in the perimedullary region, but they also occur in the phloem and/or cortex. Their size and distribution show a considerable range in different genera and species, so that they are of definite taxonomic value, but allowance must be made for the fact that transverse sections taken at different levels in a single internode of a given species often exhibit considerable differences in the number and distribution of the canals. It is, therefore, necessary to examine sections from the corresponding region of internodes of twigs of the same age when comparing genera or species. Even then it must be appreciated that there may be variations between different twigs from a single species. Before the taxonomic significance of the resin canals in the young stem can be fully assessed a thorough reinvestigation is most desirable. The resin canal system extends from the axis via the petiole and passes out into the lamina of the leaf beside the vascular bundles of the veins. For the occurrence of resin canals in the secondary xylem see below. Also important are the usually triangular **phloem** strands in the axis, with the apex towards the exterior. Each phloem strand is stratified into alternating fibrous and unglified zones. The portions of the rays traversing the phloem are also triangular with their apices towards the interior. This structure recalls that of the Malvales. **Cortical vascular bundles** are also especially characteristic of the young axis. The **hairs** are simple, unicellular, sometimes tufted, or of various glandular types. **Stomata**, confined to the lower surface of the leaf, are sometimes accompanied by subsidiary cells, but

these are not always well defined. In a few instances they are rubiaceous. The smaller **veins** of the leaf are vertically transcurrent. Although three separate vascular bundles enter the base of the **petiole**, transverse sections through the distal end exhibit a closed or very slightly open ring of vascular bundles surrounding a central medullary region with accessory bundles embedded in it. The petiolar vascular structure is always complex, and exhibits a range of structure which might prove to be of considerable diagnostic value after further investigation. Other features of specific diagnostic value are: (i) The presence or absence of mucilage cells in the leaf epidermis. (ii) The occurrence of fibres in the mesophyll.

(ii) WOOD

Vessels usually medium-sized, exclusively solitary or with some radial multiples of 2 or 3 cells, often with a slight oblique pattern; perforations simple, intervacular pitting alternate and moderate-sized to rather large, pits to ray cells often large, elongated and simple; members usually of medium length, sometimes moderately long. **Parenchyma** usually abundant and most commonly including both paratracheal (usually aliform) and apotracheal (diffuse) types, with either predominant; sometimes almost exclusively paratracheal, and then sometimes very sparse. **Rays** most commonly up to 4–8 cells wide, exclusively uniseriate in *Marquesia* and *Monotes*; often more than 1 mm. high; uniseriate few to numerous; rays heterogeneous to almost homogeneous. **Fibres** with simple or bordered pits, of medium length to moderately long. **Vasicentric tracheids** present in many genera. Vertical **intercellular canals** characteristic of all the genera except *Marquesia* and *Monotes*; radial canals occasionally present in addition.

LEAF

Dorsiventral. **Hairs**. (i) Simple, unicellular trichomes with thick walls and narrow lumina. (ii) Tufted hairs. (iii) Peltate glands, of various types but resembling those of the Oleaceae, recorded in certain species of *Anisoptera* (Fig. 51), *Doona*, *Hopea*, *Monoporandra*, *Parashorea*, *Pentacme*, *Shorea*, *Vateria*. (iv) Stalked glands with more or less lobed, unicellular heads also present in certain species of *Anisoptera*, *Dryobalanops*, and *Hopea*. (v) Glandular hairs, with multicellular, peltate heads in *Vateria* sp. Disk-shaped **extra-floral nectaries** recorded on the adaxial surface of the foliage leaves and on the abaxial surface of the stipules of *Shorea* sp. Cells of the **epidermis** small, polygonal in surface view; palisade-like in *Vateria* sp.; mucilaginous in *Balanocarpus heimii* King and certain species of *Dipterocarpus*, *Doona*, *Hopea*, *Shorea*. **Stomata** confined to the lower surface; surrounded by more or less distinct subsidiary cells, the latter being particularly well defined and parallel to the pore (rubiaceous) in some species of *Balanocarpus*, *Shorea*, and *Vateria*. Medium-sized **veins** usually, if not always, vertically transcurrent. Vascular system of the **petiole** (Fig. 53 A–D) always exhibiting a very complex structure in transverse sections through the distal end, and including a number of resin canals accompanying the vascular strands. Variations in the vascular structure and in the number and distribution of resin canals are apparently highly distinctive in different genera and species, some indication of the range being shown in Fig. 53. (In so far as there is a generalized type

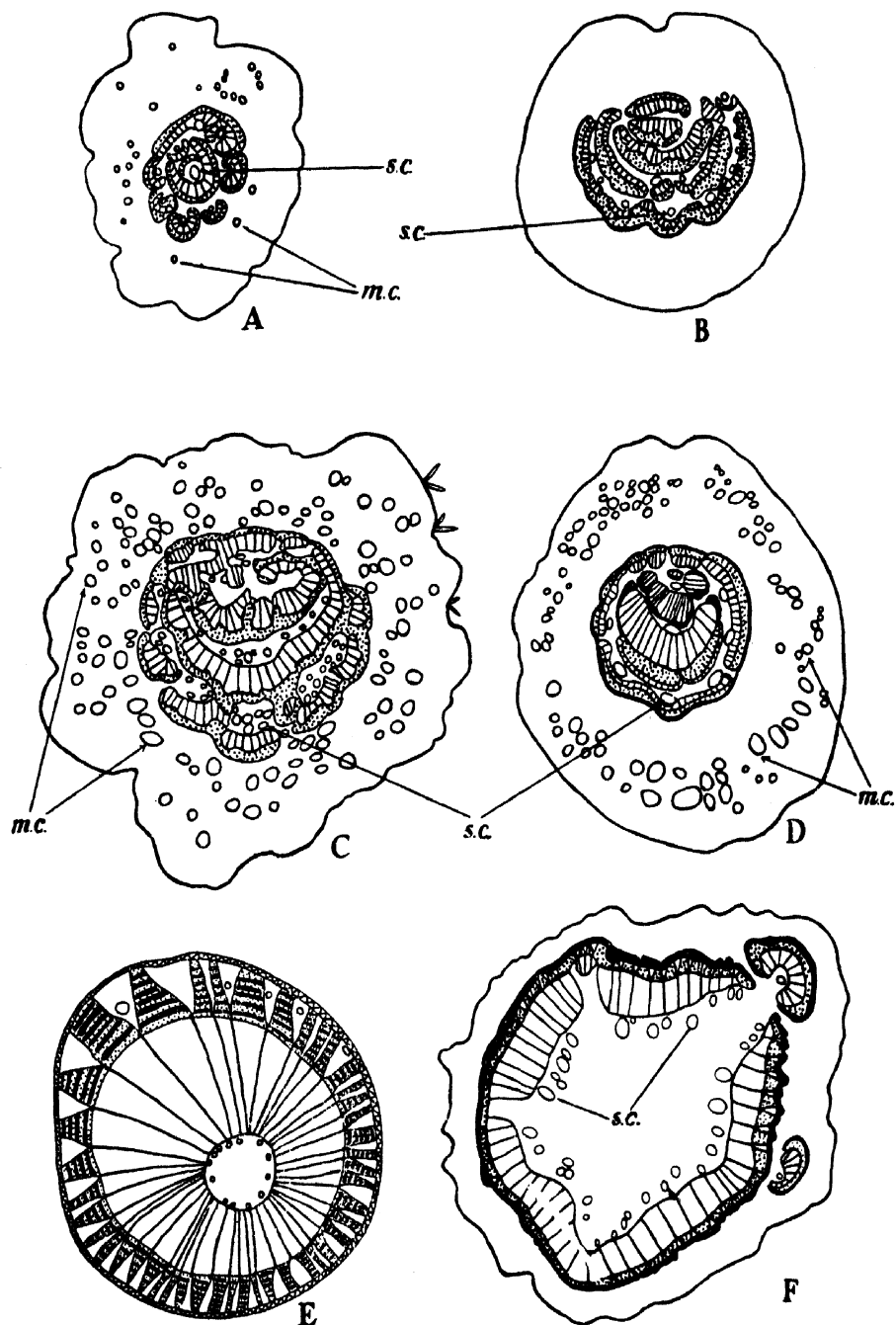


FIG. 53. DIPTEROCARPACEAE

A, *Anisoptera oblonga* Dyer. Petiole $\times 18$. B, *Isoptera sumatrana* v. Sl. Petiole $\times 23$. C, *Dipterocarpus turbinatus* Gaertn. Petiole $\times 15$. D, *Vateria indica* Linn. Petiole $\times 18$. E, *Hopea odorata* Roxb. Stem $\times 13$. F, *Anisoptera oblonga* Dyer. Stem $\times 13$.

m.c. Mucilage cells. s.c. Secretory canals.

it is usually characterized by an outer, usually somewhat interrupted, ring or arc of bundles surrounding an elaborate conducting system in the medullary region. A thorough reinvestigation of the petiolar structure of the Dipterocarpaceae, based on accurately named material, should yield data of the highest diagnostic value. Meanwhile the synopsis given by Solereder (pp. 140-3) may be consulted.) **Mucilage cells** sometimes in rows, situated in the ground tissue of the petiole and/or midrib and lateral veins in *Balanocarpus heimii* and certain species of *Dipterocarpus*, *Doona*, *Hopea*, *Parashorea*, *Shorea*, *Vateria*, and *Vatica*. **Resin canals** often found associated with the outer part of the xylem of the larger veins and in the petiole. **Crystal-idioblasts**, with mucilaginous inner membranes and containing solitary crystals, situated immediately below the upper epidermis in *Doona*, but next to the lower epidermis in *Hopea*. Cluster and, more rarely, solitary crystals commonly present and frequently abundant in the parenchymatous tissues of the mesophyll and petiole.

AXIS

YOUNG STEM (Fig. 53 E-F)

Cork, in the limited number of species investigated, originating in the epidermis itself or the outermost layer of the cortex. **Cortex** sometimes containing stone cells. **Phloem** in triangular strands (Fig. 53 E) (not always well defined in herbarium material) with the narrow portion outwardly directed, each group consisting of alternating bands of fibres and parenchyma when sufficiently mature (cf. *Tilia*). **Xylem**, in transverse sections, appearing as a more or less continuous ring. Vessels with simple perforations. **Cortical vascular bundles** (Fig. 53 F), either concentric or half-moon shaped, each accompanied by fibres in the phloem and a resin canal associated with the xylem, are especially characteristic of the family. **Mucilage cells** and **cavities** have been recorded in the cortex and pith of *Balanocarpus heimii* King and certain species of *Dipterocarpus*, *Doona*, and *Shorea*. **Resin canals** always present in the pith, but varying in number and position in different genera and species. (i) A single resin canal or a group of canals produced by the division of a single one in *Dryobalanops*. (ii) Confined to the perimedullary region, being always closely associated with the primary xylem groups in the remainder of the family. About 100 present in *Dipterocarpus*, and 3 to 30 in the remaining genera. For a synopsis of the number and distribution of resin canals in the axis in individual genera see the details given by Solereder (pp. 140-3).

WOOD (Figs. 54-5)

Vessels typically medium-sized (100-200 μ mean tangential diameter) to large (more than 200 μ), but small (less than 100 μ) in some species of *Cotylelobium*, *Hopea*, *Monotes*, and *Vatica*; almost exclusively solitary in *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Marquesia*, *Monotes*, *Upuna*, and *Vatica*; mostly solitary, but with a few pairs and short radial multiples, in the other genera; often with an oblique pattern, particularly in *Vateria*, *Vatica*, and in a few species of *Hopea*, e.g. *H. nervosa* King, *Parashorea*, e.g. *P. lucida* (Miq.) Kurz., and *Shorea*, e.g. *S. bentongensis* Foxw. and *S. bracteolata* Dyer. Usually about 3-7 per sq. mm., but distinctly more

numerous (15–26) in *Monotes* and *Vatica*. Perforations simple, horizontal or slightly oblique. Intervascular pitting alternate, typically moderate-sized to rather large, but small in *Balanocarpus heimii* King and *Hopea*; the apertures often elongated; vested; typically with some large, round to elongated,

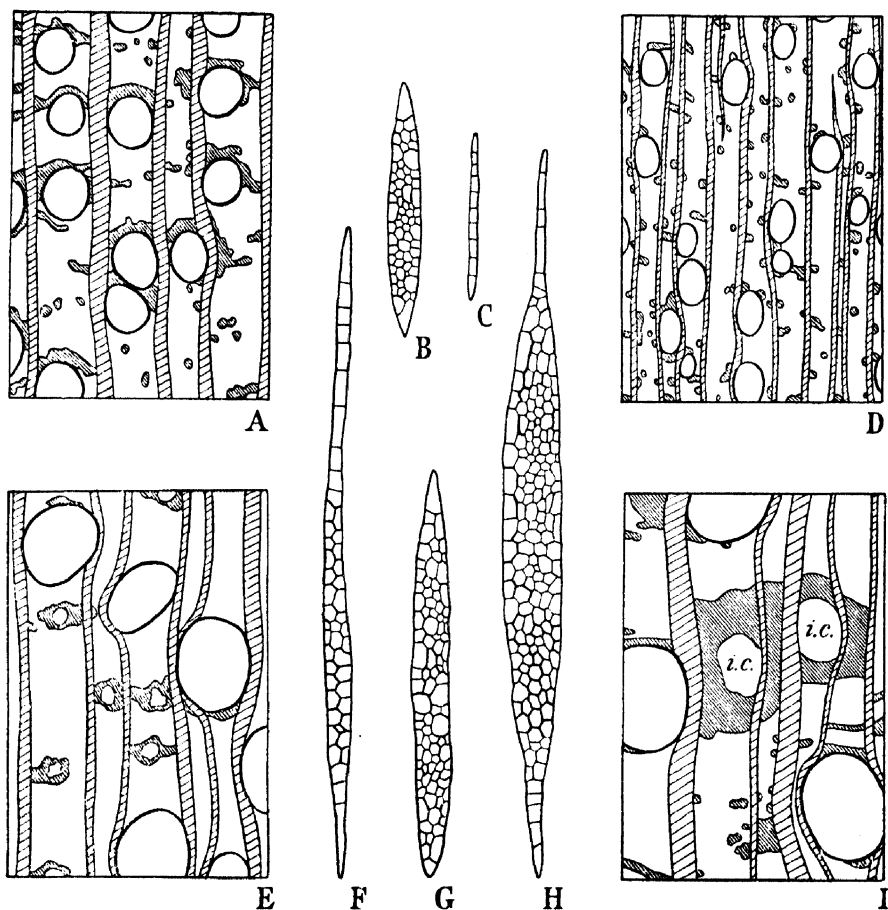


FIG. 54. DIPTEROCARPACEAE

A, *Hopea semicuneata* Sym. B, *Balanocarpus heimii* King. C, *Monotes africana* A. DC. D, *M. kerstingii* Gilg. E, *Dipterocarpus crinitus* Dyer. Showing small intercellular canals. F, *D. rotundifolius* Foxw. G, *Hopea odorata* Roxb. H, *Dipterocarpus obtusifolius* (Miq.) Teysm. I, *D. turbinatus* Gaertn. i.c. Intercellular canal.

simple pits to ray cells; pits to wood parenchyma cells occasionally scalariform; large pits rare in *Marquesia* and *Monotes*. Tyloses usually very abundant, except in *Dipterocarpus*, and often pitted. Mean member length usually 0.4–0.7 mm.; longest (up to 1.1 mm.) in *Dipterocarpus*.

Parenchyma typically with both scattered (apotracheal) and aliform (paratracheal) types and usually abundant. Both types abundant and neither predominant in *Anisoptera*, *Dipterocarpus* p.p., e.g. *D. alatus* Roxb. and *D.*

grandiflorus Blanco, *Hopea* p.p., e.g. *H. odorata* Roxb., and *Pentacme siamensis* (Miq.) Kurz. (see Fig. 55 H); the paratracheal parenchyma typically aliform in these genera, but mostly vasicentric in several species of *Dipterocarpus*. Predominantly apotracheal, as scattered cells and short tangential lines in *Anisoptera* p.p., e.g. *A. laevis* Ridl. and *A. scaphula* (Roxb.) Pierre, *Cotylelobium*, *Marquesia*, most specimens of *Monotes* (Fig. 54 D) (predominantly aliform and abaxial in some specimens), a few species of *Shorea*, e.g. *S. talua* Roxb., and *Upuna* (573). Predominantly paratracheal (aliform), (a) with moderately numerous scattered cells or short apotracheal bands (Figs. 54 A and 55 D) in *Anisoptera* p.p., *Balanocarpus heimii* King, *Doona*, *Dryobalanops*, *Hopea* p.p. (the scattered parenchyma particularly characteristic of the *Euhoepa* group, e.g. *H. helferi* (Dyer) Brandis, *H. odorata* Roxb. and *H. semecuneata* Sym., but also present in the *Pierrea* group), *Shorea* p.p., e.g. *S. robusta* Gaertn. f. and *S. palembanica* Miq., and *Vatica*; and (b) with little apotracheal parenchyma (Fig. 55 A) in *Hopea* p.p., particularly species of the *Bracteata* and *Dryobalanoides* groups, *Parashorea* and *Shorea* p.p., e.g. *S. assamica* Dyer forma *globifera* (Ridl.) Sym., *S. bentonensis* Foxw. and *S. dealbata* Foxw. Very sparse and almost entirely paratracheal, apart from the parenchyma associated with the intercellular canals (Figs. 54 E and 55 C), in some species of *Shorea*, e.g. *S. dasyphylla* Foxw., *S. leprosula* Miq., and *S. ovalis* (Korth.) Bl., and *Dipterocarpus*, e.g. *D. crinitus* Dyer. Distinctly banded in a few species of *Shorea*, e.g. *S. maxwelliana* King and *S. sericeifolia* Fischer et Hutch. Chambered crystals present in at least some species of *Hopea* (*Dryobalanoides* section), *Parashorea*, *Pentacme*, *Shorea* p.p. (particularly the 'Balau' group), and *Vateria*. Druses present in *Vateria*. Strands most commonly of 4 cells, but sometimes up to 8 cells in some species of *Anisoptera*, *Cotylelobium*, and *Vatica* and occasionally in *Dipterocarpus*; strands of 2 cells common in some species of *Hopea*. Parenchyma also occurs surrounding the intercellular canals, often in continuous bands, and occasionally as apparently terminal bands. **Rays** exclusively uniseriate in *Marquesia* and *Monotes*, typically up to 4–8 cells wide in the other genera, though occasionally slightly more than 8 cells wide in some species of *Anisoptera* and *Shorea* and seldom more than 3 cells wide in some species of *Dipterocarpus* and *Doona*; very variable in height even within a genus, often more than 1 mm. high and sometimes up to 6 mm.; uniseriates moderately numerous and composed mostly of square to upright cells in *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Doona*, *Shorea* p.p., *Vateria*, and *Vatica*, rather few and composed of square to upright and procumbent cells in the other genera; usually between 5 and 9 rays per mm., but more numerous (12–17) in *Marquesia* and *Monotes*; most commonly heterogeneous (Kribs's Types II A and B), with 1–4 marginal rows of square to upright cells, but almost homogeneous (Kribs's Type I) in a few species of *Parashorea* and *Shorea*, and homogeneous (Kribs's Type III) in *Marquesia* and *Monotes*; sheath cells sometimes present in *Anisoptera*, *Balanocarpus*, *Dipterocarpus*, *Hopea*, *Vateria*, and *Vatica*; with upright cells interspersed among the procumbent cells in some species of *Hopea* (*Euhoepa* and *Pierrea* groups) and *Balanocarpus heimii* (see Fig. 54 B). Solitary crystals common in the ray cells of some species of *Cotylelobium*, *Hopea*, *Pentacme*, *Vateria*, and *Vatica*; druses present in *Vateria*. Silica reported (794) in some species of *Anisoptera*,

Cotylelobium, *Dipterocarpus*, and *Dryobalanops* and by Desch (573) as characteristic of the 'Meranti Pa'ang' (*Anthoshorea*) group of *Shorea*, e.g. *S. sericeiflora* Fischer et Hutch., and all species of *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, and *Dryobalanops*; Besson records high percentages of silica

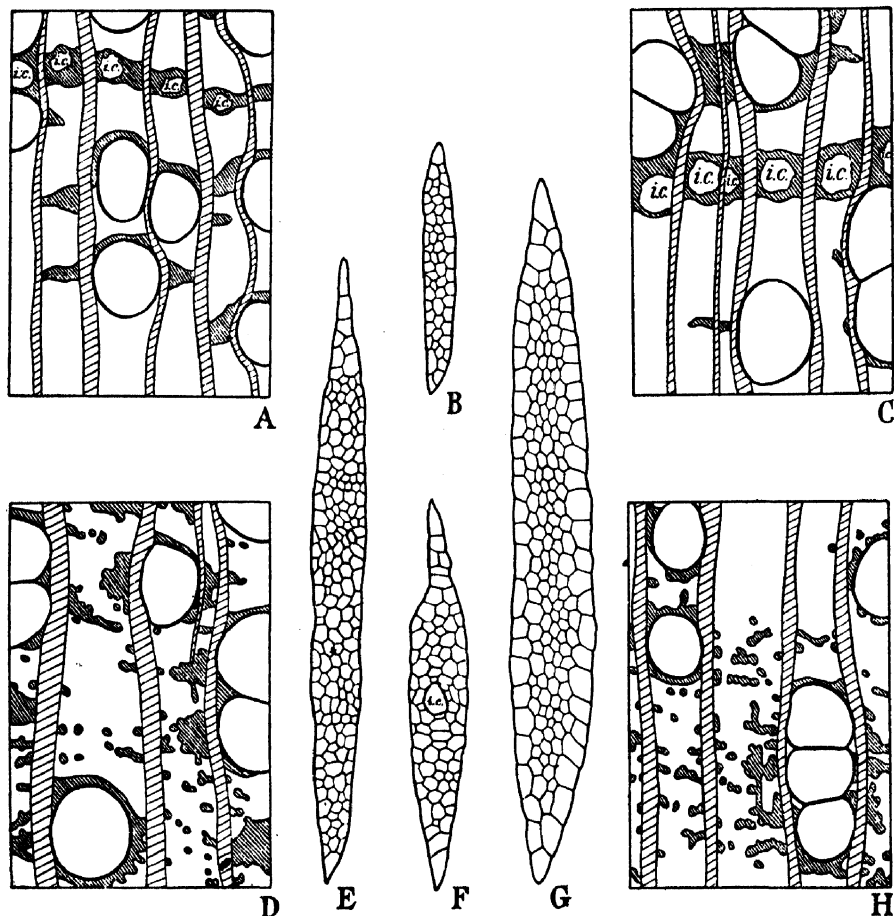


FIG. 55. DIPTEROCARPACEAE, A-H

A, *Shorea multiflora* (Burck.) Sym. T.S. B, *S. laevis* Ridl. Ray. C, *S. leprosula* Miq. T.S. D, *S. robusta* Gaertn. f. T.S. E, *S. macrantha* Brandis. Ray. F, *S. faguetiana* Heim. Ray. G, *Anisoptera laevis* Ridl. Ray. H, *Pentacme (Shorea) siamensis* (Miq.) Kurz. T.S.
i.c. Intercellular canal.

in *Dipterocarpus* sp. and *Anisoptera cochinchinensis* Pierre. **Fibres** with moderately conspicuous bordered pits in both radial and tangential walls in *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Marquesia*, *Monotes*, *Upuna*, and *Vatica*; pits simple or indistinctly bordered and tending to be mostly in the radial walls in the other genera.¹ Walls typically thick to very thick, except in some species of *Shorea*. Mean length 1.2–2.0 mm.; longest

¹ Janssonius (1154) describes the pits in *Dipterocarpus*, *Hopea*, *Shorea*, and *Vatica* as more numerous on the tangential walls.

in *Dipterocarpus*. **Vasicentric tracheids** present in *Balanocarpus heimii*, *Doona*, *Hopea*, *Parashorea*, *Pentacme*, and *Shorea*, and occasionally in *Dipterocarpus*, the cells irregular in shape and with conspicuous bordered pits. Cells intermediate between vasicentric tracheids and fibre-tracheids occur round the vessels in some of the other genera, particularly *Anisoptera*, *Dryobalanops*, and *Marquesia*. **Intercellular canals** of the vertical type present in all the genera except *Marquesia* and *Monotes*; scattered through the wood singly or in tangential series of 2-7 in *Anisoptera*, *Cotylelobium*, *Dipterocarpus* (Fig. 54 E and 1), *Vateria*, and *Vatica*, and occasionally in tangential lines particularly in *Anisoptera* and *Dipterocarpus*; typically in tangential lines in the other genera. The canals typically smaller than the vessels, but occasionally as large or larger, e.g. in *Anisoptera laevis* Ridl., *Dipterocarpus concavus* Foxw., *Shorea balanocarpoides* Sym. (573), and some species of *Vatica*. Radial canals occur in the rays of *Balanocarpus heimii* and some species of *Shorea* and *Vateria* (Fig. 55 F); according to Desch (573), they are characteristic of the 'meranti damar hitam' group of *Shorea*, e.g. *S. balanocarpoides*, and a few of the species of the 'red meranti' group, e.g. *S. leprosula*. **Growth rings**. The seasonal development of the growth rings in *Shorea robusta* Gaertn. f. has been described by Chowdhury (414).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

If the genera *Ancistrocladus* and *Lophira*, which were included by Bentham and Hooker in the Dipterocarpaceae, be omitted, the remainder of the family is anatomically very well defined. The peculiar structure of the petiole, the presence of resin canals and cortical bundles, and the triangular phloem groups stratified into sclerified and soft portions are especially characteristic features. It is interesting to note the similarity of the phloem, and to a lesser extent the structure of the petiole, to those of the Malvales.

(ii) FROM WOOD STRUCTURE

Desch (573), in his work on the Malayan Dipterocarpaceae has distinguished fifteen groups; these he combines into four tribes, which include the following genera: I. *Anisoptera*, *Cotylelobium*, *Upuna*, and *Vatica*. II. *Dipterocarpus*. III. *Dryobalanops*, and IV. *Balanocarpus*, *Hopea*, *Parashorea*, *Pentacme*, and *Shorea*. He suggests that the *Euhopea* section of *Hopea*, together with *Hopea ferrea* Lannesan and *Balanocarpus heimii* King may possibly represent a further separate tribe. He regards tribes I and II as distinctly more primitive than IV.

The different species of *Shorea* exhibit a wide range of variation, and Desch, commenting that 'unlike most other genera of the Dipterocarpaceae, *Shorea* is not a natural genus' distinguishes six groups, which he treats as if they were separate genera.

Monotes and *Marquesia* are distinguished from the rest of the family by the absence of intercellular canals and by their exclusively uniseriate rays.

Vestal (2329), in a study of the Guttiferae and their allies, has suggested that the family Dipterocarpaceae 'stems in the Exalbuminosae of the Ochnaceae, with the connecting genus probably *Lophira*'. He also holds the view that 'although the Dipterocarpaceae have occasionally been allied to the

Guttiferae due to the presence of the secretory canals', the latter should be regarded as a parallel development.

ECONOMIC USES

Most of the members of this family are medium-sized to large trees and their timbers are very widely used for general purposes in the countries in which they grow. The timbers vary from soft and light, e.g. the Malayan Red Meranti (*Shorea leprosula* Miq. *et al.*), to hard, heavy, and durable woods such as are furnished by some species of *Hopea*, some forms of 'Balau' (*Shorea* spp.), and Chengal (*Balanocarpus heimii* King). A few of them are moderately well known on world markets, e.g. Meranti (*Shorea* spp.) and Keruing (*Dipterocarpus* spp.) from Malaya, Apitong (*Dipterocarpus* spp.) from the Philippines, the Serayas and Lauans from Borneo and the Philippines (*Shorea* and *Parashorea* spp.); and Gurjun (*Dipterocarpus griffithii* Miq. and *D. turbinatus* Gaertn. f.) from India; but on the whole the woods tend to lack distinctive character and none of the species furnish outstanding special-purpose timbers. The large size and good form of the logs from most species and a tendency to gregariousness help to increase the popularity of these woods as general-purpose timbers.

Dammars and resins are obtained from the trunks of species of *Balanocarpus*, *Hopea*, *Shorea*, and *Vateria*, and oil and fat from the kernels or nuts of *Isoptera* and *Shorea*. Camphor occurs as a natural deposit in the wood of *Dryobalanops*.

GENERA DESCRIBED

(i) GENERAL ANATOMY

Anisoptera,* *Balanocarpus*,* *Dipterocarpus*,* *Doona*,* *Dryobalanops*,* *Hopea*,* *Isoptera*,* *Monoporandra*,* *Parashorea*,* *Pentacme*,* *Shorea*,* *Stemonoporus*,* *Vateria*,* *Vatica*.*

* Represented in the Kew slide collection.

(ii) WOOD STRUCTURE

Anisoptera, *Balanocarpus*, *Cotylelobium*, *Dipterocarpus*, *Doona*, *Dryobalanops*, *Hopea*, *Marquesia*, *Monotes*, *Parashorea*, *Pentacme*, (*Upuna*), *Vateria*, *Vatica*.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Gilg 771.

(ii) *On Wood Structure*

Bailey 78, Bancroft 125, 126, 127, 128, Bausch 154, Beekman 167, den Berger 179, 180, 182, 183, Besson 186, Bianchi 194, Chowdhury 411, 414, 417, Clarke 428, Desch 569, 570, 571, 573, 574, 575, Foxworthy 704, 705, Gonggrijp 794, Gupta 848, 849, Hale 870, Howard 1088, Janssonius 1154, Jones 1191, Kanehira 1206, 1209, Lecomte 1334, Méniard 1491, Pearson and Brown 1679, Record 1780, 1783, 1801, 1809, 1843, 1851, Reyes 1927, Schneider 2044, Stone 2206, Vestal 2329.

61. ANCISTROCLADACEAE

(FIG. 52 on p. 208)

SUMMARY

A family of scandent shrubs, consisting of the single genus *Ancistrocladus*. They occur for the most part in tropical Asia, although at least one species is known from the African tropics.

LEAF

Dorsiventral. **Peltate glands** (Fig. 52), visible to the naked eye and which secrete wax, occur in depressions in the surface of the leaf, the heads of the glands being close to the leaf surface conceal the pits in which they are situated. **Stomata** (Fig. 52) confined to the lower surface; actinocytic. **Hypoderm** sometimes present. **Mesophyll** including more or less distinct palisade tissue. **Veins** with vascular bundles vertically transcurrent. Three separate bundles enter the base of the leaf, but unite to form a closed or more or less open tube throughout the midrib; generally accompanied by 5-19 accessory, inversely orientated bundles situated in the outer part of the zone of fibres around the main vascular strand.

AXIS

YOUNG STEM

Cork arising at various levels in the cortex or outer part of the pericycle. **Pericycle** at first parenchymatous, but provided with a continuous or interrupted ring of stone cells when older. **Phloem** not stratified into fibrous and parenchymatous portions as in the Dipterocarpaceae, but containing stone cells, often branched and sometimes vertically elongated. Groundwork of **xylem** composed of fibre-tracheids. Vessels mostly solitary, tending to be in radial or oblique rows in some species. Wood parenchyma well developed, usually in tangential bands. Solitary and clustered **crystals** present in the primary cortex and pith. Van Tiegem's record of secretory canals in the pericycle was an error. Isolated thick-walled **secretory cells** also occur in the primary cortex.

TAXONOMIC NOTES

The genus *Ancistrocladus* was included by Bentham and Hooker in the Dipterocarpaceae, but it is now generally placed in a special family. The anatomical structure confirms that it differs somewhat from the Dipterocarpaceae. The position of the family is not well established.

GENUS DESCRIBED

Ancistrocladus.

LITERATURE

On General Anatomy
Gilg 778.

62. CHLAENACEAE

(FIG. 50 on p. 208)

SUMMARY

Shrubs or trees, confined to the Mascarene Islands. The wood exhibits the following characters. **Vessels** exclusively solitary, perforations simple, intervacular pitting alternate. **Parenchyma** apotracheal, diffuse. **Rays** exclusively uniseriate. **Fibres** very to extremely short.

LEAF

Leaf dorsiventral. **Hairs** (Fig. 50). (i) Simple, unicellular, thick-walled. (ii) Unicellular, thin-walled, twisted at the apex. (iii) Two-armed, unicellular. (iv) Peltate. (v) Multicellular, glandular, of various types. Cells of the **epidermis** polygonal as seen in surface view. **Stomata** surrounded by a rather large number of ordinary epidermal cells; sometimes in depressions, e.g. in *Schizoclaena* (Fig. 50 A); confined to the upper surface according to Gérard (757) and to the lower surface according to Solereder. **Hypoderm** of 1-2 layers sometimes present; well developed in *Schizochlaena*. **Mesophyll** including sclereids according to Beauvisage (163). Vascular bundles of the **veins** always accompanied by sclerenchyma; vertically transcurrent in *Rhodochlaena*, *Sarcochlaena*, and *Schizochlaena*. **Petiole** examined only in *Eremochlaena* by Beauvisage (163), according to whose account the vascular strand appears, in transverse sections, in the form of a closed ring surrounding a fairly large, central, medullary strand. **Mucilage cells** present in the mesophyll; those in *Eremochlaena* described by Beauvisage as very large. Cluster **crystals** recorded by the same author in the mesophyll and cortical region of the petiole in *Eremochlaena*.

AXIS

YOUNG STEM

Primary **cortex** including sclerotic cells in *Eremochlaena* and *Schizochlaena*. **Pericycle** containing groups of fibres, fairly widely separated in most genera, but almost continuous in *Sarcochlaena*. **Xylem** and **phloem** forming closed cylinders, traversed by narrow rays. Primary phloem containing 1-4 layers of fibres. Secondary phloem stratified into fibrous and parenchymatous portions. Vessels isolated or in small groups, up to about 40 μ in diameter, circular or oval; perforations simple. Paratracheal parenchyma sometimes well developed. Wood fibres provided with thick walls and bordered pits. Perimedullary region sclerosed in *Eremochlaena*. **Pith** containing sclerified cells of varying abundance, the sclereids especially numerous in *Sarcochlaena*. Pith almost entirely collenchymatous in *Xerochlamys*. Cluster **crystals** always present in the soft tissues, especially numerous in *Xerochlamys*. **Mucilage cells**, varying in frequency in different species, generally occur in the primary cortex and pith. Mucilage cells tend to disappear as the stems grow old, and are sometimes absent from *Schizochlaena*.

WOOD¹

Vessels of medium size (100–200 μ mean tangential diameter), exclusively solitary, 8–16 per sq. mm., perforations simple, intervascular pitting alternate. **Parenchyma** apotracheal, as isolated cells scattered among the fibres. **Rays** exclusively uniseriate, less than 1 mm. high, 16–18 per mm. **Fibres** with moderately thick walls; mean length about 0.5 mm.

TAXONOMIC NOTES

The presence of mucilage cells in the cortex, and the complex structure of the vascular system of the petiole suggest that this family may have affinities with the Dipterocarpaceae. It differs from the Dipterocarpaceae, however, in the absence of resin canals. Gérard (757) points out that the mucilage cells of the pith recall those which occur in certain of the Malvaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Although they are not all mentioned by name in the text, the above description of leaf and young stem is based mainly on Gérard's (757) study of the following genera: *Eremochlaena* (especially *E. humboldtiana* Baill.), *Leptochlaena*, *Rhodochlaena*, *Sarcochlaena*, *Schizochlaena*, *Xerochlamys*, *Xylochlaena*.

(ii) FOR WOOD STRUCTURE

(*Leptochlaena*), (*Rhodochlaena*).

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Gérard 757.

(ii) *On Wood Structure*

Lecomte 1333, Perrot 1694.

63. MALVACEAE

(FIG. 56 on p. 224; FIG. 57 on p. 228; FIG. 60 on p. 244)

SUMMARY

(i) GENERAL

Herbs and shrubs, widely distributed throughout the world. The stellate **hairs** are especially characteristic, but simple unicellular or uniseriate, peltate and glandular trichomes also occur. **Mucilage cells** are very common in the parenchymatous tissues, and should not be confused with the **secretory glands** with brown contents which also occur, but less frequently. The cells of the epidermis, especially in the leaf, sometimes have mucilaginous inner walls and appear as transparent dots. The **leaf** is dorsiventral in most instances although exceptions occur. **Stomata** are present on both surfaces. The **petiole** usually contains a circle of about 6, but sometimes more, separate, collateral vascular strands; but in a few instances the xylem and

¹ Based entirely on the descriptions given by Lecomte (1333) and Perrot (1694).

phloem appear, in transverse sections, as a continuous ring. **Cork** in the axis arises in the epidermis itself, or in the outermost part of the cortex. Stone cells are rarely present in the cortex. The **pericycle** of the young stem usually contains strands of fibres opposite the phloem groups, although in a few instances there is a tendency for the fibres to form a closed cylinder. The **phloem**, in most instances, is especially characteristic, consisting of triangular strands as seen in transverse sections with the bases towards the xylem, and stratified tangentially into alternating fibrous and non-fibrous bands. The

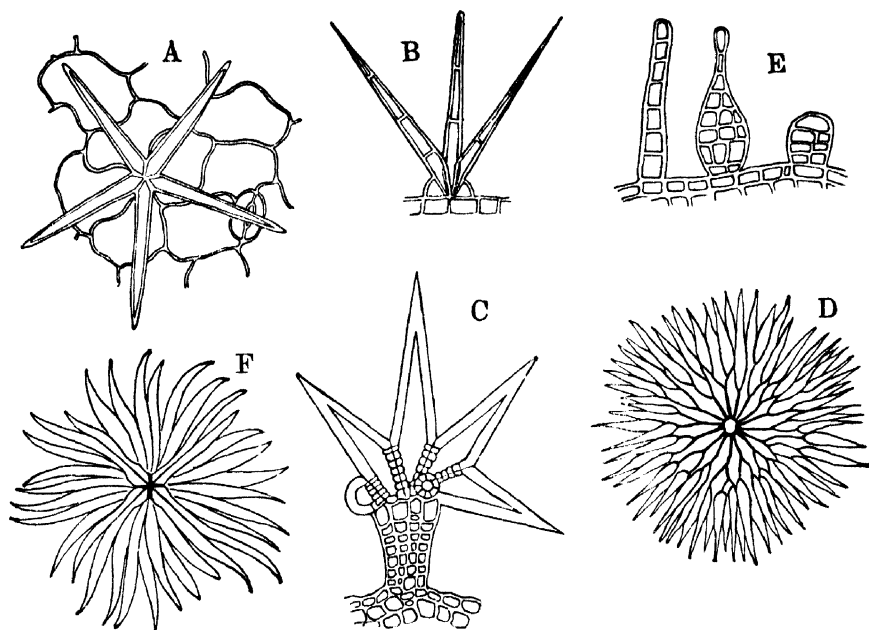


FIG. 56. MALVACEAE, A-E; STERCULIACEAE, F

A, Stellate hair of *Althaea officinalis* L. B, Stellate hair of *Malachra radiata* L. C, Stellate hair of *Malvastrum asperum* Garcke. D, Peltate hair of *Durio lanceolatus* Mast. E, Hairy covering of *Malvastrum capense* Garcke.—A, After Vogl; B-C and E, After Kuntze; D, After O. Bachmann. F, Peltate hair of *Heritiera macrophylla* Wall.—After O. Bachmann.

primary medullary rays, where passing through the phloem, are also triangular but with the apices towards the xylem. The triangular shape of the phloem groups is not very well defined in a few species. The **xylem** of the young stem usually forms a practically continuous ring, except where broken by the rather broad primary rays. The **pith** generally consists of thin-walled parenchyma, but in a few genera there are fibres in the perimedullary region. **Medullary bundles** recorded in one species of *Abutilon*.

(ii) Wood

Vessels small to medium-sized; semi-ring-porous and with spiral thickening in some genera; perforations simple, intervacular pitting small and alternate, pits to parenchyma sometimes simple and larger than the intervacular pitting; members of medium length to very short. **Parenchyma**

(a) in the Malveae and Ureneae, predominantly paratracheal, vasicentric to confluent, (b) in the Hibisceae, predominantly apotracheal, in numerous, often short bands 1-2 cells wide, accompanied by some paratracheal parenchyma; occasionally intermediate between paratracheal and apotracheal; terminal parenchyma sometimes present; fusiform cells often present; usually storied. **Rays.** Often tending to be of 2 distinct sizes; multiseriate rays usually up to 4-9 and occasionally up to 23 cells wide; low to high; uniseriate numerous to few; typically heterogeneous and often composed of mingled upright and procumbent cells, but occasionally almost homogeneous; commonly with sheath cells; druses occasionally present; storied when short and sufficiently numerous. **Fibres** with simple pits, sometimes storied, of medium length to moderately long. **Vascular tracheids** reported in 3 genera. **Intercellular canals** of the vertical traumatic type present in a few species; with 'gossypol cavities' in some species of *Gossypium* and possibly in *Thespesia*.

LEAF

Generally dorsiventral, but centric structure recorded in *Malva parviflora* Linn., occasionally isobilateral (see 'Mesophyll' below). Covered externally with characteristic stellate and tufted **hairs** (Fig. 56 A-D and 60 A), but small peltate scales, bristles and glandular hairs are to be found, several of these types sometimes occurring together in a single species. Peltate hairs recorded in *Hibiscus* and *Thespesia*. X-shaped hairs recorded on the lower surface of *Malvaviscus arboreus* Cav. by Gehrig (753). Multicellular, capitate glandular hairs of various sizes and shapes occur in species of *Gossypium*, *Hibiscus*, *Kokia*, *Lagunaria*, *Thespesia*; smaller glandular hairs, composed of fewer cells, in species of *Althaea*, *Hibiscus*, *Malva*, *Pavonia*; pitcher- or flask-shaped glandular hairs frequent in *Malva*, *Malvastrum*, *Wissadula*; depressed glands recorded in *Althaea officinalis* Linn. **Extra-floral nectaries**, consisting of groups of secretory trichomes, situated either on the surface or in concavities or depressions, recorded on the lower side of the midrib or three principal veins in certain species of *Cienfuegosia*, *Decaschistia*, *Dicellostyles*, *Gossypium* (not in *G. tomentosum* Nutt. ex Seem.), *Hibiscus*, *Ingenhouzia*, *Julostylis*, *Kydia*, *Thespesia*, *Urena*. Their shape and distribution stated by Janda (1143), Koernicke (1265), and Stanford and Viehoever (2184) to be of limited taxonomic value owing to the variation occurring within a single species. Small, inflated, refractive, spherical, multicellular glands were observed especially near the veins on the lower surface of the leaves of *Hibiscus manihot* Linn. growing at Kew; the appearance being very striking and beautiful as seen under the binocular microscope. (These are probably similar to the 'intumescences' on the leaves of *H. vitifolius* Linn. described by Dale (534). Dale's experiments led to the conclusion that the intumescences are pathological structures formed only in a sufficiently humid atmosphere and when the temperature and light conditions are appropriate.) Glandular hairs stated by Solereder sometimes to serve as **hydathodes**. The hairs on the leaf of *Abutilon* sp. reported by Luckan (1399) to be capable of absorbing water. For further details of hair structure see articles by Rousseau (1963), Sabnis (1977), Ulbrich (2308), Youngman and Panda (2499, 2500). Cells of the **epidermis** with straight or undulating anticlinal walls; some of them, especially on the upper surface, specialized for the secretion of mucilage, the large cells

sometimes penetrating into the mesophyll, e.g. in a few species of *Althaea*, *Malvaviscus*, and *Pavonia*. Mucilage cells in the epidermis inconspicuous or lacking in *Erioxylum*, most species of *Gossypium* (but fairly numerous in *G. kirkii* Mast. and *G. klotzschianum* Anderss.), *Kokia*, fairly numerous in species of *Hibiscus*, *Lagunaria*, *Thespesia*. Scattered epidermal cells with purplish or reddish cell sap present in most species of *Gossypium*, more widely distributed in plants with reddish than with green leaves. **Stomata** ranunculaceous; always present on the lower and frequently on the upper surface as well; present on both surfaces in most species of *Gossypium*, although always more numerous on the lower side, the relative frequency on the upper and lower surface respectively varying from species to species. **Hypoderm** said to be well developed in *Lagunaria patersonii* G. Don. Water-storage cells stated by Alexandrov (12) to occur in *Gossypium*. **Mesophyll**. Palisade tissue recorded as present on both surfaces in certain species of *Althaea* and *Gossypium*. *Hibiscus cannabinus* Linn. from Java is stated by Magitt (1414) to be provided with palisade tissue towards both surfaces, but palisade tissue observed only towards the upper side of leaves of the same species from Persia. Isolated sclerenchymatous elements recorded in the mesophyll of certain species of *Goethea* and *Pavonia*. Vascular bundles of the larger **veins** seldom accompanied by sclerenchyma except in the *Ureneae* and in *Hibiscus*; smaller veins vertically transcurrent or embedded in the mesophyll. **Petiole**, in transverse sections through the distal end, generally exhibiting isolated collateral bundles arranged in a circle, e.g. in *Abutilon* (strands rather close together), *Althaea* (Fig. 60 c), *Malva*, *Pavonia*, *Sida*, *Sidalcea*; but the xylem forms a closed ring in *Abutilon* (pro parte), *Anoda*, *Hibiscus* (Fig. 60 b), *Lavatera*, *Sphaeralcea*. A solitary arc-shaped bundle present in *Hoheria sexstylosa* Colenso. The vascular system, in transverse sections through the middle of the petiole of *Gossypium*, has the form of a closed ring, an arc, or a circle of isolated bundles. The number of bundles, where these are separate, varies in different species, but there are often about 6; sometimes of 2 distinct sizes in *Lavatera* and *Malva*. **Mucilage receptacles** occur in the mesophyll, e.g. in a few species of *Hoheria* and *Plagianthus*. Lysigenous '**secretory glands**' (cavities) with brown contents, not to be confused with the mucilage cells just described, sometimes appearing as transparent or dark opaque spots in the leaves, present in *Gossypium*. (When the glands are present in parts of the plant exposed to the light, the surrounding envelope of cells is believed to contain **anthocyan**, partly or wholly in the form of the glucosides quercimeritrin or isoquercitrin, or in ethereal oils, resins, or tannins. **Gossypol** occurs in the glands when not exposed to light.) Similar glands, but fewer in number, also recorded by Stanford and Viehoveer (2184) in *Cienfuegosia*, *Erioxylum*, *Ingenhousia*, *Pavonia*, *Sida*, and *Thespesia*. **Crystals**, mostly clustered but sometimes solitary, generally present; druses often very abundant although none observed at Kew in a few species of *Malva*. H-shaped crystals, in addition to ordinary druses, recorded in the *Ureneae* by Gehrig (753).

Exposure of seeds or very young seedlings of cotton to X-radiation under suitable conditions is stated by Singh, Choudri, and Kapoor (2106) to induce the petioles during subsequent development to become grooved or dorsiventral, and the vascular bundles to assume the form of a closed ring instead

of the usual circle of separate bundles. Variegation, puckering, and the development of tumours and variations in the vascular system of the lamina have also been induced by the same treatment. For detailed structure of the leaf in different species of *Lavatera* and *Malva* see Rousseau's (1963) article and for the leaf of the family in general Gehrig's (753) thesis.

AXIS

YOUNG STEM (Fig. 60 F-G)

Cork arising in the epidermis or the outermost part of the cortex. **Cortex** generally with collenchymatous and parenchymatous zones. Stone cells present in the cortex of certain species of *Goethea*, *Pavonia*, and *Sphaeralcea*. **Pericycle** always containing fibres, usually in groups external to the phloem, but sometimes tending to form a ring. **Phloem** in triangular strands with the narrow portions outwardly directed; more or less distinctly stratified owing to the presence of tangential bands of fibres. The triangular shape of the phloem groups is more apparent in some genera than in others. The pericycle and phloem of many Malvaceae yield commercial fibres (see 'Economic Uses'). The primary medullary rays also triangular where traversing the phloem but with the base towards the exterior. **Xylem** forming a practically continuous ring in most instances, except where traversed by the broad, primary, medullary rays, e.g. in *Malva sylvestris* Linn. (Fig. 60 G). Vessels with simple perforations. **Pith** generally consisting of thin-walled parenchyma, but containing sclerenchymatous fibres situated on the inside of the xylem in certain species of *Hoheria*, *Matisia*, and *Plagianthus*. **Mucilage cells** and cavities present in the cortex and pith; especially numerous in species of *Althaea*, *Anoda*, *Cristaria*, *Hoheria*, *Kitaibelia*, *Lavatera*, *Malope*, *Malva*, *Napaea*, *Palava*, *Sida*; less numerous in species of *Abutilon*, *Fugosia*, *Goethea*, *Gossypium*, *Hibiscus*, *Kydia*, *Lagunaria*, *Malachra*, *Malvaviscus*, *Pavonia*, *Sidalcea*, *Sphaeralcea*, *Thespesia*, *Urena*, *Wissadula*. **Secretory glands** (cavities) with brown contents, similar to those in the leaf, occur in the cortex of *Cienfuegosia*, *Erioxylum*, *Gossypium*, *Ingenhouzia*, *Pavonia*, *Sida*, *Thespesia*. (For further particulars see 'Leaf'.) **Mucilage canals** recorded in the pith of a few species of *Hibiscus*, *Kokia*, *Thespesia*. Cluster **crystals** very common and frequently abundant in the cortex, phloem, rays, and pith, but the frequency varies in different species; those in the phloem sometimes smaller than those in the other tissues; probably occurring in most genera, and definitely observed in species of *Abutilon*, *Althaea*, *Gossypium*, *Hibiscus*, *Hoheria*, *Lagunaria*, *Malva*, *Pavonia*, *Sida*, *Sidalcea*, *Sphaeralcea*. Large solitary crystals sometimes present as well as the clusters although less frequently, e.g. in species of *Hoheria* and *Lagunaria*. Crystals sometimes more abundant in very young than in slightly older stems, e.g. in the pith of very young stems of *Abutilon insigne* Planch. Small spherical outgrowths or **papillae**, with walls at first containing pectic substances but subsequently becoming cutinized, described by Blackwell (202) as arising from the pith of *Althaea rosea* Cav. when wounded. **Callus formation** in wounded stems of *Hibiscus rosa-sinensis* Linn. stated by Sharples and Gunnery (2084) to originate from the exposed medullary ray cells, the cambium playing a part only after the initial formation of a callus cushion.

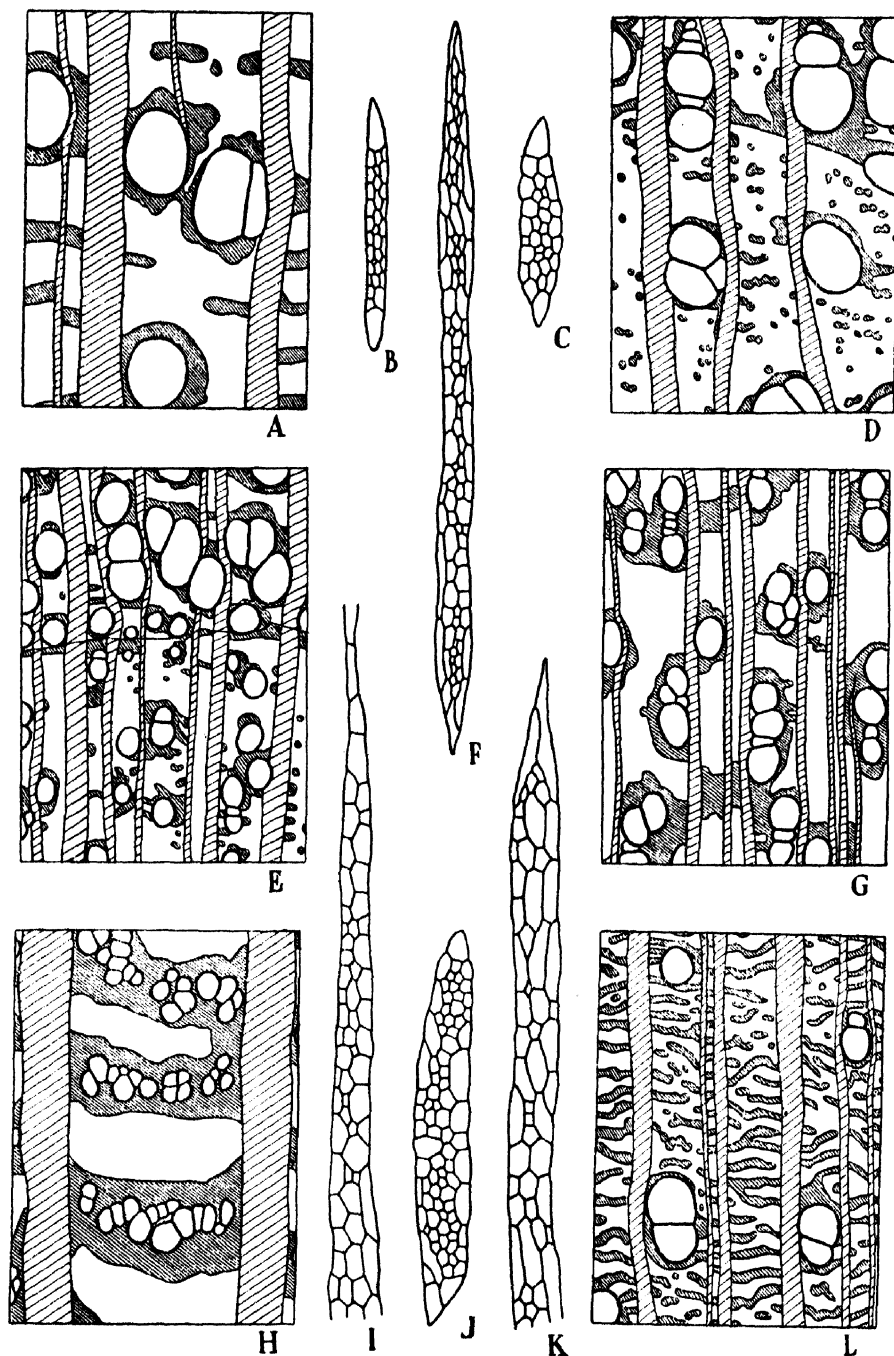


FIG. 57. MALVACEAE

A, *Kydia calycina* Roxb. B, *Cephalohibiscus peekelii* Ulbricht. C, *Hibiscus elatus* Sw. D, *H. elatus* Sw. E, *Gossypium thurberi* Tod. F, G, *obtusifolium* Roxb. G, *Abutilon niveum* Griseb. H, *Hoheria populnea* A. Cunn. I, *Malvaviscus mollis* DC. J, *Thespesia populnea* (L.) Soland. K, *Gossypium morilli* Cook et Hak. L, *Thespesia populnea* (L.) Soland.

WOOD (Fig. 57)

Vessels small (less than $100\ \mu$ mean tangential diameter) or medium-sized ($100\text{--}200\ \mu$), the latter mostly less than $150\ \mu$ in diameter; extremely small (less than $25\ \mu$) in *Sphaeralcea* (2373), very small ($25\text{--}50\ \mu$) in some species of *Abutilon*, *Alyogyne*, *Althaea* (2373), *Cienfuegosia* (2373), *Erioxylum*, *Hoheria*, *Lavatera*, *Malvastrum* (2373), *Pavonia* (2373), *Plagianthus*, *Shantzia* (2373), *Tetrasida*, and *Wissadula* (2373), moderately small ($50\text{--}100\ \mu$) in some species of *Abutilon*, *Bastardiopsis*, *Gossypium*, *Hibiscus*, *Hoheria* (2373), *Lagunaria*, *Malvastrum*, *Pavonia*, *Shantzia*, *Sida*, and *Urena*, largest (about $150\ \mu$) in some species of *Hibiscus*, *Kydia*, and *Paritium*, and, according to Solereder, in *Plagianthus sidoides* Hook.; solitary, in irregular clusters and in radial multiples of 2 or 3; multiples commonly of 4 or more cells present in some species of *Abutilon*, *Hibiscus*, *Lavatera*, *Malvastrum*, *Malvaviscus*, *Pavonia*, *Sphaeralcea*, and *Urena* and sometimes producing a radial pattern in *Lavatera* and *Malvastrum*; sometimes with a rather vague tangential pattern in *Abutilon* and *Lavatera*, entirely limited to the tangential arcs of parenchyma separating the fibres into groups in *Hoheria* (Fig. 57 H) and *Plagianthus* and intermediate in *Sphaeralcea*; except in the woods with pronounced pattern or multiples, seldom more than 20 per sq. mm.; 5–10 per sq. mm. in some species of *Bombycidendron*, *Erioxylum*, *Gossypium*, *Hibiscus*, *Paritium*, and *Thespesia*, fewer than 5 per sq. mm. in *Cephalohibiscus*, *Gossypium*, *Hibiscus*, *Kokia* (2373), *Kydia*, *Thespesia* (2373) and *Wercklea*, up to 30 per sq. mm. in *Tetrasida*; ring-porous or semi-ring-porous in some species of *Gossypium*, *Hibiscus*, *Malvastrum*, *Paritium*, *Sida* (2430), *Sphaeralcea*, and *Thurbergia*; spiral thickening observed in the small vessels of some species of *Abutilon*, *Hibiscus* (rare), *Hoheria*, *Malvastrum*, *Plagianthus*, *Sida* (1851), *Sphaeralcea*, *Thurberia*, and *Wissadula* (2373). Perforations simple. Intervascular pitting alternate, sometimes with some much elongated slit-like pits, e.g. in *Malvastrum* p.p., and sometimes striated owing to coalescent apertures, e.g. *Gossypium dryparioides* Seem.; Webber (2373) describes the pitting as alternate, opposite or occasionally scalariform in part; small to minute; pits to ray and wood parenchyma typically similar to the intervacular pitting but sometimes simple, and with some horizontally or obliquely elongated pits in some species of *Abutilon*, *Cephalohibiscus*, *Hoheria*, *Lavatera*, *Malvaviscus*, and *Wercklea* and particularly in *Pavonia* p.p., *Plagianthus*, and *Sphaeralcea*. Most of the genera with occasional deposits of gum (2373); tyloses observed only in *Bombycidendron* and *Hibiscus*. Mean member length $0.2\text{--}0.7$ mm., mostly, according to Webber (2373), $0.33\text{--}0.45$ mm. **Parenchyma** rather scanty to abundant; predominantly paratracheal in the Malveae and Ureneae: vasicentric to slightly aliform in *Abutilon* p.p., *Malvastrum* p.p., *Malvaviscus*, *Pavonia*, *Sida* p.p., and *Urena*, aliform to confluent in *Abutilon* p.p., *Bastardiopsis*, *Lavatera*, *Sida* p.p., and *Tetrasida*, confluent in *Hoheria*, *Malvastrum* p.p., *Plagianthus* and *Sphaeralcea*; with numerous biseriate apotracheal bands predominating in *Kydia* (Fig. 57 A); in *Lavatera*, in addition to the paratracheal parenchyma, there are occasional broad bands of very thin-walled parenchyma cells, sometimes numerous locally or linking up to form a ground-tissue in which, in cross-section, the groups of fibres and vessels appear as small islands or bands; in *Urena* there are numerous small groups of thin-walled cells (apparently composed of fusiform parenchyma cells) scattered

over the cross-section in a manner similar to that of the strands of included phloem in *Strychnos*; single specimens of *Malvaviscus mollis* DC. and *Pavonia spicata* Cav. were observed to have predominantly apotracheal parenchyma of the type described below for the *Hibisceae* and to differ in this respect from other species of these genera. Apotracheal parenchyma always present and often predominant in most of the *Hibisceae*: in numerous, short bands 1–2 cells wide in *Alyogyne*, *Cephalohibiscus*, *Dicellostyles* (2373), *Erioxylum*, *Gossypium* (rare in some species), *Hibiscus*, *Juliostylis* (2373), *Paritium*, *Shantzia*, *Thespesia* (Fig. 57 L), and *Wercklea*, and with more regular and more continuous bands in some specimens of *Gossypium* and *Hibiscus*; the paratracheal parenchyma more prominent and tending to be aliform in some of the species of *Hibiscus*, *Paritium*, and *Thurberia*; particularly in the late wood, in broader bands, intermediate between metatracheal and confluent in *Lagunaria* and possibly in *Kokia* (2373); vasicentric or aliform and without apotracheal parenchyma in *Bombycidendron*. Terminal parenchyma present in some genera. According to Webber (2373), frequently with crystals in *Althaea*, *Bombycidendron*, *Hibiscus*, *Kokia*, and *Thespesia*, and with yellow, reddish, or brown gum in *Althaea*, *Gossypium*, *Hibiscus*, *Kokia*, *Kydia*, *Malvaviscus*, and *Thespesia*. Strands most commonly of 2–4 cells, tending to be mostly of 2 cells in the *Malveae*, though Webber states that they are up to 8 cells in *Kydia*. Fusiform cells moderately common in many of the genera. Storied in nearly all the species, except in very small stems. **Rays** very variable in type, ranging from (a) high multiseriate rays composed mainly of narrow upright cells, together with numerous uniseriate rays, to (b) large homogeneous rays with few uniseriates, or (c) short, heterogeneous, storied rays. In the *Ureneae*—*Malvaviscus*, *Pavonia*, and *Urena*—the multiseriate rays are high, 2–5 cells wide, with relatively few procumbent cells, which are scattered among the upright cells as described by Chattaway (272) for her ‘*Pterospermum*’ type of tile cell (Fig. 57 I), and the uniseriate rays are numerous, composed entirely of upright cells, and moderately high (Kribs’s *Het.* Type I). In the *Hibisceae* similar types, though with wider multiseriate rays, occur in a few species of *Gossypium* (Fig. 57 K) and *Hibiscus* and in *Wercklea*, but in most of the woods of this sub-family that have high rays, the procumbent cells are more numerous, the upright cells are shorter and sometimes almost square (particularly in *Lagunaria*) and the uniseriate rays are few, often composed of procumbent cells and commonly only 2 or 3 cells high (Kribs’s *Het.* Type II B), e.g. in *Erioxylum*, *Gossypium* p.p., *Hibiscus*, *Lagunaria*, *Shantzia*, *Sphaeralcea*, and *Thurberia*; in other genera or species, e.g. *Bombycidendron*, *Cephalohibiscus*, *Hibiscus* p.p., and *Paritium*, the rays are low, 2–3 (occasionally 4) cells wide, heterogeneous with 1 or 2 marginal rows of upright cells, with a central part composed entirely of procumbent cells, and storied (see Fig. 57 B and C); *Thespesia* is intermediate, with most of its rays of the latter type, but with some high rays, in which procumbent and upright cells alternate (see Fig. 57 J). In the *Malveae* the tendency is towards more homogeneous rays. High multiseriate rays and relatively few uniseriates, both with alternating procumbent and upright cells, occur in *Abutilon*, *Lavatera*, *Malvastrum*, *Sphaeralcea*, but the upright cells are barely more than square in *Abutilon* and *Lavatera*; in *Hoheria* and *Plagianthus* almost all the rays are very large and composed of small procumbent cells

surrounded by sheath cells, small rays being scarce and usually uniseriate; in *Bastardiopsis* and *Kydia* the large rays are shorter and with less conspicuous sheath cells, and small rays up to 3 cells wide are numerous, storied and heterogeneous; in *Sida* all the rays are homogeneous and the storied small rays are nearly all uniseriate; in *Tetrasida* most of the rays are only 1 story high, 2-4 cells wide, homogeneous and storied, and uniseriates are rare. Rays 2-3 cells wide in some species of *Bombycidendron*, *Cephalohibiscus*, *Gossypium*, *Hibiscus*, *Malvaviscus*, *Paritium*, and *Pavonia*; up to 10-14 cells wide in some species of *Bastardiopsis*, *Hibiscus*, *Lagunaria*, and *Malvastrum*; up to 17 cells in *Hoheria* and 23 cells in *Plagianthus*; up to 4-9 cells wide in the other genera and in some species of *Gossypium*, *Hibiscus*, *Paritium*, and *Pavonia*; commonly with a tendency to be of 2 distinct sizes in the woods with larger rays; exceeding 1 mm. in height except in some species of *Abutilon*, *Bastardiopsis*, *Bombycidendron*, *Cephalohibiscus*, *Kydia*, *Paritium*, *Shantzia*, *Tetrasida*, and *Thespesia*; fewer than 5 per mm. in some species of *Hibiscus*, *Hoheria*, *Lagunaria*, and *Plagianthus*, 12-15 per mm. in *Abutilon*, *Malvaviscus*, *Pavonia*, *Tetrasida*, and *Urena*, 6-11 per mm. in the remainder; homogeneous in *Sida* and almost homogeneous in *Bastardiopsis* and *Tetrasida*; markedly heterogeneous in most of the other genera; with square or upright cells intermingled with procumbent cells and tending to alternate in groups (see Fig. 57 F, I, J, and K), as in Chittaway's (272) 'Pterospermum' type of tile cell, in *Abutilon* p.p., *Alyogyne*, *Erioxylum*, *Gossypium*, *Hibiscus* p.p. (a few specimens only), *Lavatera*, *Malvaviscus*, *Pavonia*, *Shantzia*, *Sphaeralcea*, *Thespesia*, *Thurbera*, *Urena*, and *Wercklea*; with square or upright cells (other than sheath cells) limited to 1 or 2 marginal rows in *Abutilon* p.p., *Bastardiopsis*, *Bombycidendron*, *Cephalohibiscus*, *Gossypium* p.p. (a few specimens only), *Hibiscus* p.p., *Hoheria*, *Kydia*, *Paritium*, and *Plagianthus*; with sheath cells in *Abutilon* p.p., *Alyogyne*, *Erioxylum*, *Gossypium* p.p., *Hibiscus* p.p., *Hoheria*, *Malvastrum*, *Thespesia*, *Thurbera*, and *Urena*; very commonly containing crystals, with druses in some species of *Althaea* (2373), *Lavatera*, *Paritium*, *Thurbera*, and *Sphaeralcea* and sometimes with gummy contents. Webber (2373) records the occurrence of gossypol cavities in some species of *Gossypium*. All the rays storied in *Abutilon* p.p. (according to Webber, but not in any of the 6 species examined), *Bombycidendron*, *Hibiscus* p.p., *Paritium*, *Tetrasida*, and *Thespesia* (2373); with the small rays storied in *Abutilon* (rare), *Bastardiopsis*, *Dicelostyles* (2373), *Hibiscus* p.p., *Julistylis* (2373), *Lagunaria*, *Sida*, and *Thespesia* p.p. **Fibres** typically with small simple pits, but according to Webber (2373), fibre-tracheids form a considerable portion of the wood in *Pavonia* and *Wercklea*; pits very numerous in the radial walls of *Bastardiopsis* and *Sida*. With thin walls in some species of *Cephalohibiscus*, *Gossypium*, *Hibiscus*, *Lavatera*, *Malvaviscus*, *Pavonia*, and *Urena*, and with very thin walls in *Wercklea*; with thick walls in species of *Abutilon*, *Bombycidendron*, *Hoheria*, *Kydia*, *Plagianthus*, *Sida*, *Tetrasida*, and *Thurbera*. Commonly storied in woods in which the parenchyma is distinctly storied. Mean length 0.36-2.33 mm. (2373); usually of medium length (0.9-1.6) but sometimes longer, e.g. in *Bombycidendron*, *Hibiscus* p.p., and *Hoheria*. **Vascular tracheids** reported by Webber (2373) in *Malvastrum*, *Plagianthus*, and *Wissadula*. **Intercellular canals** of the traumatic vertical type reported in species of *Hibiscus* and *Urena* by Webber (2373) who suggests that the secretory

cavities observed by Hohnel in *Thespesia populnea* (L.) Soland. may be of this type or may possibly be 'gossypol cavities'. **Growth ring** formation in *Hibiscus* has been investigated by Coster (481) in Java.

ROOT

Most completely described by Gore and Taubenhaus (796) for *Gossypium* as follows. Secondary **xylem** constituting a large proportion of the root; vessels solitary or in groups of 2-4, frequently containing conspicuous tyloses; wood fibres with thick walls, tapering ends, and bordered pits; rays 4 cells wide and many rows of cells tall; **secretory glands**, similar to those of the stem and leaf, present in the portions of the rays situated in the phloem. Concentric layers of **cork** are formed around a single vessel or group of vessels in the xylem of *Althaea officinalis* Linn. Fibres occur in the **phloem** of all the investigated genera. This character is stated by Solereder to be rare in other families with the exception of the Sterculiaceae and Tiliaceae. The root of *Althaea officinalis* is described under 'Economic Uses', and some particulars concerning the roots of *Gossypium* and *Hibiscus* given in the same section.

ANOMALOUS STRUCTURE

Medullary vascular bundles recorded by Sabnis (1977) in the pith of *Abutilon fruticosum* Guill et Perr.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Malvaceae constitute a homogeneous group from the anatomical standpoint. There is evidence that they have very close affinities with the Bombacaceae, and also, but to a less pronounced extent, with the Tiliaceae and Sterculiaceae. It will be recalled that certain genera described under Flacourtiaceae (see p. 126) are believed to have affinities with the Tiliaceae.

(ii) FROM WOOD STRUCTURE

The tribe Hibisceae (Fig. 57 D and L) appears to be clearly separated by its parenchyma from the Ureneae and Malveae (Fig. 57 G and H), but Webber (2373) states categorically that the distinction is not valid, at any rate on the basis suggested by Dumont. Webber has shown that the vessel characters indicate that the family is a fairly advanced group, and has drawn attention to the unusually wide range of variation within the genera as at present delimited and even within some species.

There are no true tile cells, but the rays of the Ureneae might represent the early stages of development leading to true tile cells, such as occur in the Durioneae of the Bombacaceae and the Buettnerieae.

ECONOMIC USES

The outstanding economic importance of this family is due to the fibres and hairs which they yield. Of these, by far the best known is cotton, which consists of the hairs attached to the seeds of several species of *Gossypium*. For modern descriptions of the anatomical structure and variations within the genus *Gossypium* see Webber's (2376) and Hector's (929) accounts. Other

important fibres are obtained from the pericycle and phloem of many members of the family, some of which are as follows. Queensland Hemp (*Sida rhombifolia* Linn.), Chinese or Indian Hemp (*Abutilon avicennae* Gaertn.), Aramina fibre from Brazil (*Urena lobata* Linn.), Rozelle Hemp (*Hibiscus sabdariffa* Linn.), Deccan Hemp (*Hibiscus cannabinus* Linn.), Cuba Bast (*Hibiscus elatus* Sw.), 'Po lom Pom' fibre (*Thespesia macrophylla* Blume), (Dantzer 540), Gambo Hemp (*Hibiscus* sp.), (Horst 1085). For details of the anatomical structure of some of these fibres see Wiesner (2423). The family also includes several well-known ornamental plants such as the mallows (*Malva* spp.), Hollyhocks (*Althaea* spp.), and *Hibiscus* spp. The leaves and roots of *Althaea officinalis* Linn. are used for medicinal purposes. The root of *Althaea officinalis* exhibits the following anatomical characters. Groups of 3–25 phloem fibres, unignified except for the middle lamella; numerous starch grains, mostly simple and ovoid; occasional cluster crystals; numerous mucilage cells, easily stained by ruthenium red.

Secondary thickening in the roots of cotton infected by *Fusarium* sp. is stated by Dharmarajulu (581) to be initiated much earlier than in healthy roots, whilst peripheral cork is especially well developed, and cells in the region of the invading mycelium become suberized in cotton plants infected by the same fungus. Twisting and hypertrophy of the vascular system, enlargement of the cortical cells and medullary rays and the more abundant deposition of crystals are induced in roots of *Hibiscus esculentus* Linn. when invaded by the eelworm *Heterodora radiculicola* according to Saran (1995). Roots of *Gossypium* grown in acid soils exhibit, according to Gore and Taubenhaus (796), proliferations which originate from the ray cells, and from a stimulation of the cambium and phloem; the original phloem sometimes being killed, but subsequently replaced by new phloem containing the usual elements but in varying proportions.

The timbers are usually light, though sometimes moderately heavy, are not very durable and are of no importance. The wood of *Thespesia populnea* (L.) Soland. is reputed to be durable under water (Desch 574); *Hibiscus elatus* Sw. furnishes a timber that is highly valued where it occurs, e.g. in Jamaica.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abutilon,* *Althaea*,* *Anoda*, *Cienfuegosia*, *Cristaria*, *Decaschistia*, *Dicellostyles*, *Fugosia*, *Goethea*, *Gossypium*,* *Hibiscus*,* *Hoheria*,* *Ingenhouzia*, *Julostylis*, *Kitaibelia*, *Kokia*, *Kydia*, *Lagunaria*,* *Lavatera*, *Malachra*, *Malope*, *Malva*,* *Malvastrum*, *Malvaviscus*, *Napaea*, *Palava*, *Pavonia*,* *Plagianthus*, *Senra*, *Sida*,* *Sidalcea*, *Sphaeralcea*,* *Thespesia*, *Urena*, *Wissadula*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Abutilon, *Alyogyne*, *Bastardiopsis*, *Bombycidendron*, *Cephalohibiscus*, (*Cienfuegosia*), *Erioxylum*, *Gossypium*, *Hibiscus*, *Hoheria*, (*Kokia*), *Kydia*, *Lagunaria*, *Lavatera*, *Malvastrum*, *Malvaviscus*, *Paritium*, *Pavonia*, *Plagianthus*, *Shantzia*, *Sida*, *Sphaeralcea*, *Tetrasida*, *Thespesia*, *Thurberia*, *Urena*, *Wercklea*, *Wissadula*.

LITERATURE

(i) *On General Anatomy*

Alexandrov 12, D'Almeida 536, Blackwell 202, Dale 534, Dantzer 540, Dharmarajulu 581, Farr 672, Gehrig 753, Gore and Taubenhaus 796, Hector 929, Hess 957, Horst 1085, Janda 1143, Kienholz 1236, Koernicke 1265, Luckan 1399, Magitt 1414, Rousseau 1963, Sabnis 1977, Saran 1995, Sharples and Gunnery 2084, Singh, Choudri and Kapoor 2106, Spieth 2169, Stanford and Viehoveer 2184, Ulbrich 2308, Webber 2376, Wiesner 2423, Youngman and Panda 2499, 2500.

(ii) *On Wood Structure*

Beekman 167, den Berger 179, 182, Brown, F. B. H. 282, Burgerstein 310, 312, Chatterway 272, Coster 481, Cozzo 494, Dadswell and Record 533, Desch 574, Edlin 622, Forsaith 690, Garratt 744, Greguss 2522, Hyde 1117, Janssonius 1154, Kanehira 1206, 1209, Lecomte 1334, Pearson and Brown 1679, Record 1781, 1787, 1801, 1809, 1843, 1848, 1851, 1885, Record and Hess 1886, Record and Mell 1894, Riera 1937, Webber 2373, Williams 2426, 2430.

64. BOMBACACEAE

(FIG. 58 on p. 238; FIG. 59 on p. 240; FIG. 60 on p. 244)

SUMMARY

(i) GENERAL

A tropical family of trees with many anatomical features in common with the Malvaceae. Such differences as there are between them appear to be mainly correlated with the more definitely arboreal habit of the Bombacaceae. Some members of the family attain an enormous size (e.g. *Ceiba pentandra* Gaertn.), while others such as the baobab (*Adansonia digitata* B. Juss.) possess barrel-shaped trunks, which, although short, reach a considerable diameter. The timber of most species is very light and soft, the most outstanding example being Balsa (*Ochroma lagopus* Sw.) (see 'Economic Products' below). On the relatively young branches and trunks of some of the species there are large, deciduous, **woody spines**. The Bombacaceae tend to be deciduous, the leaves falling in dry seasons. Some of the larger trees are supported by **buttress roots**. Peltate and stellate **hairs** are very common, whilst **mucilage**, secreted either in cells or cavities, is very characteristic of the family. The vascular structure of the **petiole** tends to be complex. The **phloem** in young stems appears as triangular strands in transverse sections, the apices of the triangles being towards the exterior. It is stratified into fibrous and non-fibrous zones. The portions of the medullary rays which traverse the phloem are also triangular but with their apices inwardly directed. Cluster **crystals** are common in the parenchymatous tissues.

(ii) WOOD

Vessels typically medium-sized to large; perforations simple, intervacular pitting alternate, small in the Durioneae and in a few genera of the Matisieae, large in the other genera; pits to parenchyma often multiples of the intervacular pits or unilaterally compound, except in some of the genera with small intervacular pitting; members of medium length to moderately short. **Parenchyma** abundant and sometimes forming the ground tissue of the wood; typically in numerous fine, metatracheal lines and in narrow sheaths round the vessels (vasicentric); with strands of 8 cells and not storied in the Durioneae; typically of 4 cells and storied in the other tribes. **Rays** of the Adansoniaceae and Matisieae typically 4–10 cells wide, 1.5 to several mm. high, 2–6 per mm. heterogeneous, with 1–2 marginal rows of upright cells in the large rays and rather few uniseriate, which are usually storied if sufficiently numerous. Rays of the Durioneae 3–10 cells wide, typically 1 to several mm. high, 7–12 per mm., heterogeneous, with 4 or more marginal rows of upright cells and numerous uniseriate rays; with tile cells, except in *Maxwellia*; uniseriate rays not storied. **Fibres** with simple or bordered pits, septate in a few genera; scanty and occupying less space than the parenchyma in several genera; commonly storied except in the Durioneae; moderately short to moderately long. **Intercellular canals** of the vertical traumatic type occur in some genera.

LEAF

Generally dorsiventral (see also 'Mesophyll'). **Hairs** sometimes absent, but peltate kinds very characteristic, recorded especially in *Bombax*, *Boschia*, *Camptostemon*, *Coelostegia*, *Cullenia*, *Cumingia*, *Dialycarpa*, *Durio*, *Neesia*, and *Quararibea*. **Extra-floral nectaries**, similar to but differing somewhat in structure from those of the Malvaceae, situated on the lower side of the midrib and on the dorsal surface of petiole in certain species of *Adansonia*, *Ceiba*, *Chorisia*, and *Pachira*. **Cuticle** often thick, occurring as high ridges in certain species of *Carolinea*, *Ceiba*, *Chorisia*, and *Pachira*. **Epidermis** many layered in certain species of *Adansonia* (Gehrig 753), *Bombax*, and *Durio*; some of the epidermal cells divided horizontally in *Chorisia* and *Quararibea* sp. **Hypoderm** present in *Durio*. **Stomata** confined to the lower surface. **Mesophyll** of the cotton tree (*Ceiba pentandra* Gaertn.) found by Magitt (1414) to be dorsiventral when grown in America, but, when grown in the Old World, possessing palisade tissue on both sides with a small amount of spongy tissue at the centre. Leaves of hybrids between plants from both sources, as well as seedling plants and greenhouse specimens of the same species stated to have the palisade tissue confined to the upper side. Isolated sclerenchymatous elements in the mesophyll recorded in *Bombax*. **Petiole**, in transverse sections, exhibiting a cylindrical vascular strand (cf. *Hibiscus* in Malvaceae) in many of the Bombacaceae, but more complex types such as a closed but lobed vascular strand or a closed strand surrounding two central strands present in certain species of *Bombax*, *Coelostegia*, and *Durio*. **Mucilage cells** situated in the epidermis, especially on the upper side, sometimes extending into the mesophyll in *Adansonia*, *Boschia*, *Durio*, and *Quararibea*.

AXIS

YOUNG STEM (Fig. 60 H)

Cork superficial in origin. **Cortex** of most genera including stone cells. Other scattered cells in the cortex, readily stained with haematoxylin, are presumably tanniniferous. **Pericycle** rather indefinitely marked by strands of fibres, mostly situated at the outer periphery of the phloem groups, but extending laterally in a few instances. **Phloem** strands, and portions of the primary medullary rays between them, appearing triangular in transverse sections. Phloem usually stratified into fibrous and non-fibrous tangential zones. **Xylem** tending to be in the form of a closed cylinder, but usually somewhat interrupted by rather broad, often lignified primary medullary rays. Vessels with simple perforations. **Pith** sometimes very broad and consisting of thin-walled spongy tissue, e.g. in *Bombax malabaricum* DC. and *Pachira macrocarpa* Walp.; at others more compact and composed of thick-walled, pitted cells, e.g. in *Camptostemon philippinensis* Becc. **Cortical bundles** observed in *Bombax malabaricum* and *Camptostemon philippinensis*. **Fruit stalks** of *Adansonia* polystelic. Cluster **crystals** usually abundant in the parenchymatous tissues; solitary crystals also occur but rather less frequently. **Mucilage cells** and **cavities**, situated in the parenchymatous tissue of the cortex and pith, are abundant in *Adansonia*, *Bombax*, *Ceiba*, *Chorisia*, and *Pachira*; rare in *Hampea*, *Ochroma*, *Quararibea*, and *Scleronema*; very rare in *Boschia*, *Coelostegia*, *Durio*. Mucilage cells sometimes arranged

in longitudinal rows. Secretory cavities, often somewhat elongated, present in the pith and in the portions of the medullary rays passing through the phloem in *Pachira* and *Durio*.

WOOD (Figs. 58-9)

Vessels typically medium-sized (100-200 μ mean tangential diameter) to large (more than 200 μ); moderately small (50-100 μ) in some species of *Camptostemon*, *Matisia*, *Maxwellia*, and *Quararibea*; about 200 μ or more in diameter in at least some species of *Adansonia*, *Bernoullia*, *Bombacopsis*, *Bombax*, *Cavanillesia*, *Ceiba*, *Chorisia*, *Coelostegia*, *Durio*, *Gossampinus*, *Huberodendron*, *Matisia*, *Neesia*, *Ochroma*, *Pachira*, and *Scleronema*; mostly solitary, with a few multiples of 2 or 3 cells, with a tendency to the formation locally of longer multiples, irregular clusters and tangential groups; mostly 0.5-5 per sq. mm., slightly exceeding this maximum in some individual specimens, about 12 per sq. mm. in *Maxwellia*. According to Record and Hess (1886) the pores are more numerous in the outer part of the growth ring in some specimens of *Bombacopsis*, *Bombax*, *Cavanillesia*, *Ceiba*, *Chorisia*, *Ochroma*, and *Pachira*. Perforations simple; intervacular pitting alternate, minute in *Camptostemon*, *Matisia*, and *Quararibea*, very small in *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, *Gyrantnera*, *Hampea*, *Maxwellia*, *Neesia*, and *Scleronema*, large in the other genera; sometimes with striations due to coalescent apertures, e.g. in *Boschia* and *Scleronema*; pits to ray and wood parenchyma cells often large, simple and unilaterally compound, less commonly so in genera with very small intervacular pitting and not observed in *Boschia* p.p., *Camptostemon*, *Coelostegia*, *Durio*, *Hampea*, *Huberodendron*, *Matisia*, *Maxwellia*, *Montezuma*, *Quararibea*, and *Scleronema*. Small amounts of gummy deposits present in some species, tyloses present and sometimes abundant in some species of *Aguaria* (1857), *Bernoullia*, *Bombacopsis*, *Bombax* (2436), *Cavanillesia*, *Ceiba*, *Chorisia*, and *Scleronema* (1857); deposits of calcium carbonate have been observed by Record (1818) in callus tissue and in dark streaks in the normal heartwood of *Quararibea* spp. Mean member length 0.3-0.8 mm. **Parenchyma** abundant (reported by Solereder to be scanty in *Pavonia*), sometimes forming the ground tissue, predominantly apotracheal, but vasicentric always present as well; in closely spaced (6 or more per mm.), regular, uniseriate (occasionally biseriate) bands, separated by 1-3 fibres, in *Adansonia*, *Bernoullia*, *Bombacopsis*, *Bombax*, *Chorisia*, *Gossampinus*, *Gyrantnera*, *Hampea*, *Matisia*, *Montezuma*, *Pachira*, and *Quararibea* (Fig. 58 E and G); in more widely spaced and less regular bands, which sometimes merge into diffuse parenchyma, in the *Durioneae*, e.g. *Boschia*, *Camptostemon*, *Coelostegia*, *Cullenia*, *Durio*, *Maxwellia*, and *Neesia*, and also in *Huberodendron* (Fig. 58 A and D); forming a continuous ground tissue, in which the fibres are interspersed in groups, in *Cavanillesia*, *Ceiba*, *Chorisia* p.p., and *Ochroma*; in widely spaced bands 2-10 cells wide (possibly terminal) in *Scleronema*, together with diffuse, vasicentric and a little aliform; in broad 5-20-celled bands, separated by narrower bands of fibres, in *Aguaria* (1857) and *Catostemma* (Fig. 59 C). A few genera with chambered crystals and others with dark gummy contents; with druses in *Adansonia* and according to Janssonius (1154) in *Ceiba*; Solereder refers to silica bodies present in *Coelostegia borneensis* Becc. and *C. griffithii* Benth. (794). Strands, in the

apotracheal parenchyma, usually of 4 cells, strands of 2 cells common in *Camptostemon*, *Hampea*, *Montezuma*, *Ochroma*, and *Scleronema*; strands seldom of less than 8 cells in the Durioneae, e.g. *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, *Maxwellia*, and *Neesia*, and in some species of *Matisia*, *Pachira*, and

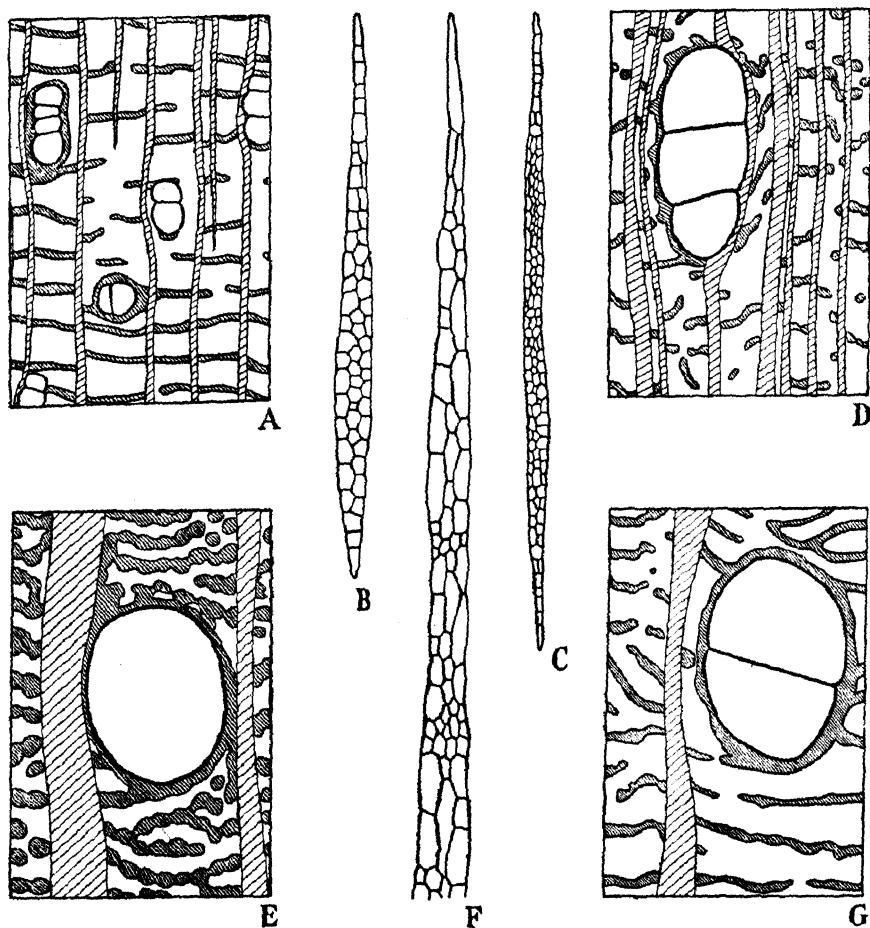


FIG. 58. BOMBACACEAE

A, *Camptostemon philippinensis* Becc. B, *Cullenia excelsa* Wight. C, *Coelostegia griffithii* Benth. D, *C. griffithii* Benth. E, *Bombax malabaricum* DC. F, *Ochroma lagopus* Sw. G, *Bernoulia flammea* Oliv.

Quararibea; fusiform cells common in *Hampea* and *Ochroma*; strands of the vasicentric parenchyma usually containing more cells than those of the apotracheal. Typically storied except in the Durioneae, but not distinctly storied in *Chorisia* p.p., *Matisia*, and *Quararibea*; storied in *Camptostemon* of the Durioneae; sometimes with secondary storying due to regular subdivision of the strands, e.g. in *Bombax*. Cells on cross-section commonly much wider than the fibres and irregular in shape, except in the Durioneae. **Rays** typically 4-10 cells wide; exclusively uniseriate in *Camptostemon*, rarely more

than 3 cells wide in *Maxwellia*, 10–15 cells wide in some species of *Aguaiaria* (1886), *Bombacopsis*, *Ceiba* (1885), *Chorisia* (1885), *Gyranthera*, *Hampea*, *Matisia*, *Quararibea*, and *Scleronema*; often described as of two distinct sizes, e.g. by Record and Hess (1886), but intermediate sizes are usually common; uniseriate rays numerous in the Durioneae, not common in the other sub-families and sometimes rare, e.g. in *Adansonia*, *Bernoullia*, *Cavanillesia*, *Gyranthera*, *Huberodendron*, *Montezuma*, *Ochroma*, and *Quararibea* p.p.; multiseriate rays typically high, often 4 mm. or more, e.g. in *Bombax*, *Catostemma*, *Pachira*, and *Quararibea*, and up to 10 mm. in *Matisia*, less than 1 mm. in some species of *Boschia*, *Huberodendron*, and *Montezuma*; typically with well-marked sheath-cells except in the Durioneae, but these cells are less pronounced in some species of *Bombax*, *Huberodendron*, and *Pachira*; 7–12 per mm. in the Durioneae, 2–11 per mm. in the other tribes, less than 4 per mm. in some species of *Adansonia*, *Bernoullia*, *Bombacopsis*, *Cavanillesia*, *Gyranthera*, *Huberodendron*, *Matisia*, and *Quararibea*, seldom exceeding 6 per mm. in the other genera except in *Matisia cordata* H.B. et K.; heterogeneous, the larger rays seldom with more than 1 or 2 marginal rows of upright cells (Kribs's Type II B) except in the Durioneae, in which the rays commonly have 4 or more marginal rows and in some species 10 or more (Kribs's Types I and II A?); homogeneous (Kribs's Type III) in *Camptostemon*; crystals occur in chambered or ordinary cells in only a few species but are sometimes abundant, e.g. in *Camptostemon* and *Matisia*; in the form of druses in *Adansonia* and *Bernoullia*; dark gum-like contents common. Large rays not storied, but small rays storied where sufficiently numerous, except in the Durioneae other than *Camptostemon*; all the rays short and storied in the latter and in one specimen of *Montezuma cubensis* Urb. **Tile cells** of the 'Durio' type (Chattaway 372) occur in all the Durioneae examined except *Camptostemon* and *Maxwellia*, i.e. in *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, and *Neesia*; an intermediate form, in which the upright cells are less narrow radially and distinctly higher axially than the procumbent cells (Chattaway's 'Pterospermum' type), occurs in *Montezuma* and *Ochroma*, both of the *Matisieae* (Fig. 58 F). In the 'Durio' type the uniseriate rays present an unusual appearance in tangential section, the procumbent cells being round and the interspersed tile cells consequently with concave walls where they abut on the procumbent cells; the small rays of *Montezuma* and *Ochroma* are also composed of alternating upright and procumbent cells, but as the upright cells are twice as wide tangentially as the procumbent cells the latter are always biseriate and in consequence wholly uniseriate rays are rare. **Fibres** with simple or indistinctly bordered pits equally numerous in both radial and tangential walls; pits more distinctly bordered and mostly in the radial walls in the Durioneae, e.g. in *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, *Maxwellia*, and *Neesia*. Septate in *Adansonia* and *Bombacopsis* and, according to Record (1857), in *Bombax*, *Hampea*, and *Pachira*. Walls very thin, e.g. in *Ochroma*, to thick in some species of *Bombacopsis*, *Matisia*, *Montezuma*, and *Pachira*, and extremely thick in *Catostemma*; the light weight of many of the woods, e.g. *Cavanillesia*, is due to the small proportion of fibres rather than to the thinness of their walls; fibres in narrow, often uniseriate lines or small groups and occupying less space than the parenchyma in *Adansonia*, *Bombax*, *Cavanillesia*, *Ceiba*, *Chorisia*,

Gossampinus, *Hampea*, *Ochroma*, and *Pachira*. Commonly storied. Mean length 0.7–2.0 mm. **Intercellular canals** of the vertical traumatic type reported by Record (1857) in *Bombacopsis*, *Bombax*, *Catostemma*, *Cavanillesia*, *Ochroma*, *Pachira*, and *Scleronema*, and by Desch (574) in *Durio*. **Growth rings**. Studies of seasonal growth have been made by Chowdhury (414) in *Bombax* and by Coster (481) in *Ceiba* and *Gossampinus*. Besson (186) notes a high ash content in the woods of *Bombax* and *Ceiba*.

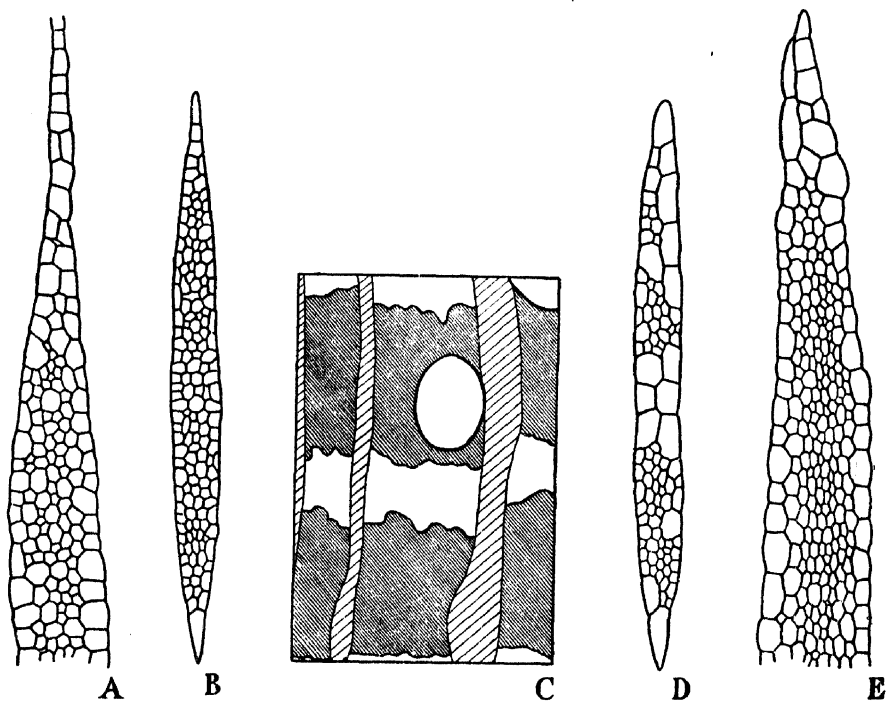


FIG. 59. BOMBACACEAE

A, *Matisia cordata* H.B. et K. B, *Durio zibethinus* Murr. C, *Catostemma fragrans* Rodrig. D, *Montezuma speciosissima* Sesse et Moq. E, *Cavanillesia platanifolia* H.B. et K.

ROOT

Navez (1582), after comparing meteorological data with the arrangement of the so-called buttress roots in *Ceiba pentandra* Gaertn., observed that the buttresses attain their maximum development on the side exposed to the prevailing wind. It was, therefore, concluded that they support the trees by acting as resistance cables rather than buttresses.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The anatomical characters indicate quite clearly that the Bombacaceae and Malvaceae are very closely related. It is interesting to note the more complex vascular structure of the petiole which seems to be associated with the arboreal habit of the Bombacaceae. The shrubby genus *Hibiscus* of the

Malvaceae, with its solitary cylindrical vascular strand, is exactly comparable with the least complex type to be found in the Bombacaceae. The anatomical structure also confirms that there are affinities with the Sterculiaceae and Tiliaceae.

(ii) FROM WOOD STRUCTURE

The tribe Durioneae is clearly distinguished from the others by its tile cells, parenchyma type, and numerous uniseriate rays. *Maxwellia*, however, though agreeing in other respects, lacks tile cells. *Camptostemon* appears from its wood structure to be out of place in this tribe.

The Matisieae are nearer to the Durioneae than are the Adansonieae. *Catostemma* stands apart on account of its parenchyma and fibres.

ECONOMIC USES

The Baobab (*Adansonia digitata* B. Juss.) is the source of a bast fibre. The Silk Cotton trees, belonging to the genera *Bombax* and *Ceiba*, yield a floss from around the seeds which arises from the wall of the fruit, and is used in the manufacture of life-saving and other equipment where buoyancy is important, as well as for upholstery purposes. The best-known floss is Kapok, derived from *Ceiba pentandra* Gaertn. For details concerning the structure of *Ceiba pentandra* Calvet's (329) Thesis may be consulted. Balsa wood is the product of *Ochroma lagopus* Sw. According to Pierce (1717) most of the so-called distinct species of *Ochroma* which yield Balsa wood are in reality ontogenetic stages or ecological varieties of the one species *Ochroma lagopus*. The nature of the indumentum on the leaf of the plant varies with age, since the indumentum is deciduous. The Durian (*Durio zibethinus* Murr.) yields edible fruits.

The timbers of this family vary from light and soft, e.g. in the Bombacineae, to heavy and hard, e.g. in the Catostemmataceae. Some of the woods are exceptionally light, particularly those derived from the genera *Aguaria*, *Cavanillesia*, *Ceiba*, and *Ochroma*, the best known of which is the Balsa, *Ochroma lagopus* Sw. The timber of *Bombax malabaricum* DC. is of some importance in the East for the match industry, and this and other species are used for tea and rubber boxes and packing-cases. In tropical America *Bombacopsis* and *Ceiba* supply timber of local utility and occasional export (1886).

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Adansonia, *Bombax*,* *Boschia*, *Camptostemon*,* *Carolinea*, *Ceiba*, *Chorisia*, *Coelostegia*, *Cullenia*, *Cumingea*, *Dialycarpa*, *Durio*,* *Eriodendron*, *Hampea*, *Matisia*, *Neesia*, *Ochroma*, *Pachira*,* *Quararibea*, *Scleronema*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Adansonia, (*Aguaria*), *Bernoullia*, *Bombacopsis*, *Bombax*, *Boschia*, *Camptostemon*, *Catostemma*, *Cavanillesia*, *Ceiba*, *Chorisia*, *Coelostegia*, *Cullenia*, *Durio*, *Gossampinus*, *Gyranthera*, *Hampea*, *Huberodendron*, *Matisia*, *Maxwellia*, *Montezuma*, *Neesia*, *Ochroma*, *Pachira*, *Quararibea*, *Scleronema*.

LITERATURE

(i) *On General Anatomy*

Braun 265, 266, Calvet 329, Gehrig 753, Little 1379, Magitt 1414, Navez 1582, Pierce 1717.

(ii) *On Wood Structure*

Benoist 169, den Berger 179, 182, Besson 186, Br. Hond. F. D. 274, Chattaway 372, Chowdhury 414, Cooper 461, Coster 481, Cozzo 494, Dadswell and Record 533, Desch 574, Ewald 666, Foxworthy 705, Gonggrijp 794, Howard 1088, Hyde 1117, Janssonius 1154, Jentsch 1172, Kanehira 1206, 1209, 1214, Kribs 1283, Lecomte 1334, Panshin 1649, Pearson and Brown 1679, Pereira 1687, Pfeiffer, J. Ph. 1713, Record 1780, 1781, 1787, 1801, 1809, 1818, 1834, 1843, 1848, 1851, 1857, 1885, Record and Hess 1886, Record and Mell 1894, Rowlee 1964, Stone 2206, Webber 2372, Williams 2430.

65. STERCULIACEAE

(FIG. 56 on p. 224; FIG. 60 on p. 244; FIG. 61 on p. 246; FIG. 62 on p. 250)

SUMMARY

(i) GENERAL

Trees or shrubs, more rarely herbs. The family occurs in tropical and sub-tropical regions. Anatomical features which recall those of the Bombacaceae and Malvaceae include: (i) The predominantly stellate **hairs**, often accompanied by simple unicellular, uniseriate, glandular, and peltate types. (ii) The usually triangular and stratified **phloem** strands of the young stem. (iii) The occurrence of **mucilage receptacles** which may be in the form of cells, cavities, or canals. The leaf is generally dorsiventral, but in a few species the mesophyll is composed entirely of palisade cells. The **stomata** are usually ranunculaceous. The main vascular strand of the **petiole** usually appears, in transverse sections, as a closed cylinder of xylem and phloem, or as a cylinder formed by a number of separate but closely situated vascular bundles. In either of these cases there are often several accessory bundles, of very varying shapes in different species, situated in the pith of the petiole. In the young stem **cork** arises from the outermost layer of the cortex; the **pericycle** contains well-developed fibre strands usually forming caps at the exterior of the phloem (see above), the xylem constitutes a closed cylinder, but is traversed by the relatively broad primary medullary rays. **Crystals** are quite frequent and secreted in the form of large clusters; solitary types also occur but are less common. Scattered cells, stained deeply with haematoxylin and presumably tanniniferous, occur in parenchymatous tissues of the stem and leaf. They have been observed in species of *Cola*, *Dombeya*, *Fremontia*, *Guazuma*, *Heritiera*, *Theobroma*, *Trochetia*, and probably occur in other genera as well. **Spines** have been recorded in *Buettneria* and *Eriolaena*.

(ii) Wood

(a) *Excluding Buettnerioideae*

Vessels medium-sized to large, few (1-5 per mm.); perforations simple, intervacular pitting alternate, small; pits to parenchyma sometimes larger and elongated; members typically of medium length, occasionally moderately short. **Parenchyma** principally of 2 types: (a) diffuse, with a little vasicentric, and (b) broad apotracheal to confluent bands, also with some

vasicentric parenchyma; terminal bands sometimes present; storied. **Rays** often of 2 distinct sizes, the larger up to 3–20 cells wide, 1–4 mm. high in most genera, uniseriate rays scarce in some genera, heterogeneous, with sheath cells; the small rays sometimes storied. **Fibres** with simple pits, storied in some genera, of medium length to very long. **Intercellular canals** of the vertical traumatic type present in a few specimens.

(b) *Buettnerioideae*

Vessels mostly medium-sized, with multiples of 4 or more cells in some genera, occasionally in large groups with a radial or oblique pattern; mostly 5–20 per mm., sometimes very numerous (more than 50 per mm.); with a tendency to be ring-porous in several genera; occasionally with spiral thickening; perforations simple, intervascular pitting alternate, small, pits to parenchyma similar in size and shape; members of medium length to very short. **Parenchyma** of 2 alternative types: (a) diffuse, with a little vasicentric, and (b) exclusively paratracheal, vasicentric, aliform, or locally confluent; storied in most of the genera. **Rays** often of 2 distinct sizes, the larger mostly 4–10 cells wide and commonly exceeding 1 mm. in height, typically heterogeneous, but almost homogeneous in a few genera, commonly with sheath cells; the small rays often storied and the rays predominantly storied in some genera; tile cells present in several genera. **Fibres** with small simple pits, storied in some genera, of medium length.

LEAF

Generally dorsiventral, but palisade and spongy mesophyll not always clearly differentiated; mesophyll consisting wholly of palisade tissue in *Melhania* spp. according to Sabnis (1977) and in *Reevesia*, but composed mainly of spongy tissue with only a little palisade in *Heritiera littoralis* Ait. according to Kienholz (1236). **Hairs**, like those of the Malvaceae, consisting of simple unicellular, uniseriate, glandular, tufted, stellate, and peltate types. Peltate hairs recorded particularly in species of *Cheirolaena*, *Dombeya*, *Heritiera* (Fig. 56 F) (whole of the lower surface covered with overlapping scales in *H. littoralis*), *Tarrietia*, *Trochetia*. One of each pair of **stipules** in *Pterospermum javanicum* Jungh. becoming hollow and lined with short-stalked glandular bodies so as to have the function of **extra-floral nectaries**. **Cuticle** sometimes thick in *Sterculia*. Cells of the **epidermis** commonly mucilaginous, especially in *Sterculia*. One layer of **hypoderm** recorded in *Ungeria* by Zebe (2504) and 3 layers in *Heritiera littoralis* by Kienholz (1236). **Stomata** similar to those of the Malvaceae, generally ranunculaceous, but said by Zebe (2504) to be rubiaceous in *Reevesia*; confined to the lower surface in species of *Cola*, *Guazuma*, *Sterculia*, and *Theobroma* examined by Gehrig (753). **Midrib** including sclerenchyma in the species of *Cola*, *Guazuma*, *Sterculia*, and *Theobroma* examined by Gehrig (753). **Petiole** supplied by a vascular system appearing, in transverse sections, as a closed ring of xylem and phloem (Fig. 60 D), or a circle of closely placed but separate bundles, in certain species of *Abroma*, *Cheiranthodendron*, *Dombeya*, *Guazuma*, *Heritiera*, *Hermannia*, *Kleinhovia*, *Lasiopetalum*, *Pterospermum*, *Sterculia*, *Theobroma*; vascular structure as above but often enclosing one to several accessory bundles embedded in the pith in *Cola*, *Heritiera* (Fig. 60 P), *Sterculia*, and *Theobroma*.

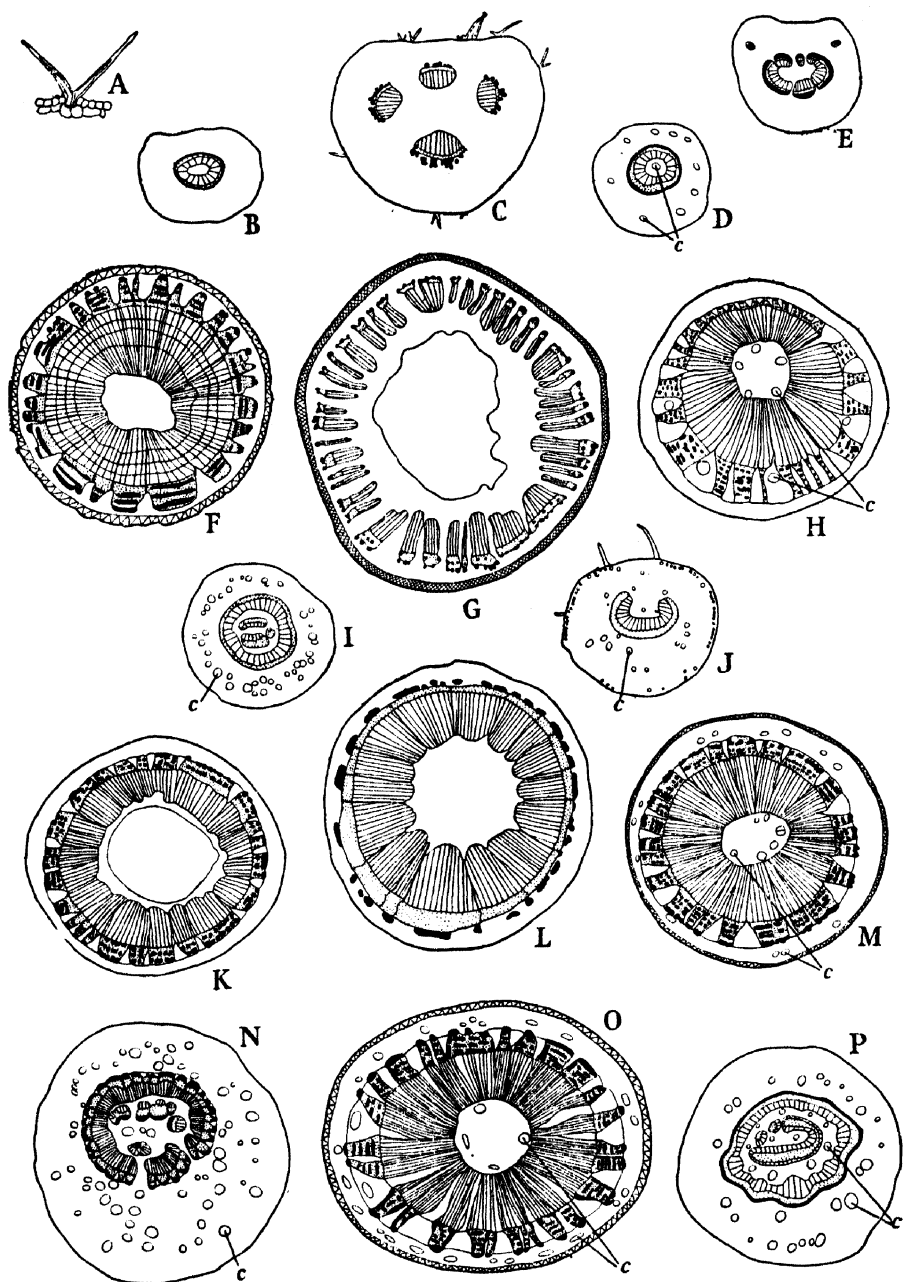


FIG. 60. **MALVACEAE**, A-C and F-G; **STERCULIACEAE**, D and N-P; **ELAEOCARPACEAE**, E and L; **BOMBACACEAE**, H; **TILIACEAE**, I-K and M

A, *Althaea officinalis* Linn. Typical hair $\times 90$. B, *Hibiscus syriacus* Linn. Petiole $\times 15$. C, *Althaea officinalis* Linn. Petiole $\times 12$. D, *Guazuma tomentosa* H.B. et K. Petiole $\times 13$. E, *Aristotelia macqui* L'Hérit. Petiole $\times 13$. F, *Hibiscus syriacus* Linn. Stem $\times 10$. G, *Malva sylvestris* Linn. Stem $\times 7$. H, *Durio zibethinus* Murr. Stem $\times 12$. I, *Tilia vulgaris* Hayne. Petiole $\times 13$. J, *Corchorus olitorius* Linn. Petiole $\times 13$. K, *C. olitorius* Linn. Stem $\times 12$. L, *Aristotelia macqui* L'Hérit. Stem $\times 13$. M, *Tilia vulgaris* Hayne. Stem $\times 13$. N, *Theobroma cacao* Linn. Petiole $\times 10$. O, *T. cacao* Linn. Stem $\times 10$. P, *Heritiera macrophylla* Wall. Petiole $\times 10$.

c. Mucilage cavity.

(Fig. 60 N), the medullary bundles sometimes forming an almost complete inner ring in *Heritiera*: vascular strand in the form of an arc with strongly incurved ends in *Fremontia mexicana* Macbride.

The above observations and records concerning the petiolar vascular structure of the Sterculiaceae have recently been considerably amplified by the investigations of Dehay (558, 559). This author found transverse sections through the middle rather than the distal end of the petiole to be the most useful for diagnostic purposes, and, in species with a complex system of medullary bundles, there are considerable variations in structure depending on the level at which the sections are taken.

Dehay's central type of petiolar structure for the Sterculioideae exhibits a vascular strand consisting of an adaxial and an abaxial arc almost united to form a ring, and enclosing a central concave, collateral medullary strand with adaxial xylem, e.g. in *Sterculia tragacantha* Lindl. (This type also occurs in certain members of the Tiliaceae.) In *Sterculia acerifolia* A. Cum. the medullary system is reduced, and from *S. foetida* Linn. it is absent. The medullary system is, on the other hand, progressively more complex in the series *Sterculia carthaginensis* Jacq., *Cola altissima* Engl., and *Pterygota aubrevillei* Pellegr.

Dehay also recognizes a distinct central type for the Buettnerioideae, consisting of a deeply concave vascular crescent with the ends very much incurved, e.g. in *Commersonia echinata* var. *platiphylla* Forst. This type also occurs in *Mansonia altissima* A. Chev. One modification of this central type is represented by petioles in which adaxial portions of the strand appear, in transverse sections, as partly independent strands, e.g. in *Commersonia bartramia* Merr. In other species the adaxial portions of the vascular system appear, again in transverse sections, to be completely independent of the main abaxial strand. The abaxial xylem then appears circular and is accompanied by 2 smaller circles of xylem towards the adaxial side. All 3 circles of xylem are embedded in phloem. This type occurs in *Reevesia pubescens* Mast. In *Scaphopetalum blackii* Mast., an adaxially concave vascular cylinder is accompanied by 2 cortical strands towards the wings and encloses a solitary, centric strand with central phloem. In *Theobroma grandiflorum* Sch. and other species of *Theobroma* the main abaxial arc is accompanied by a complex adaxial system.

The Sterculioideae and Buettnerioideae are not, however, sharply demarcated by their petiolar structure since certain species of *Dombeya* (e.g. *D. malacoxylon* Sch.), *Hua*, *Pterospermum* (e.g. *P. diversifolium* Bl.), and *Theobroma* exhibit vascular systems resembling those of the Sterculioideae.

Mucilage (see also 'Stem') as in the Malvaceae, commonly present in special **cells**, **cavities**, or **canals** situated in the ground tissue of the petiole, but cells and cavities more widely distributed than canals. Clustered and solitary **crystals** generally present in the mesophyll, the former type being especially large in *Rulingia* sp. **Tannin** abundant.

AXIS

YOUNG STEM (Fig. 60 O)

Cork arising in the outermost layer of the cortex. **Cortex** sometimes containing stone cells in *Cola*, *Tarrietia*, and *Ungeria*. **Pericycle** including

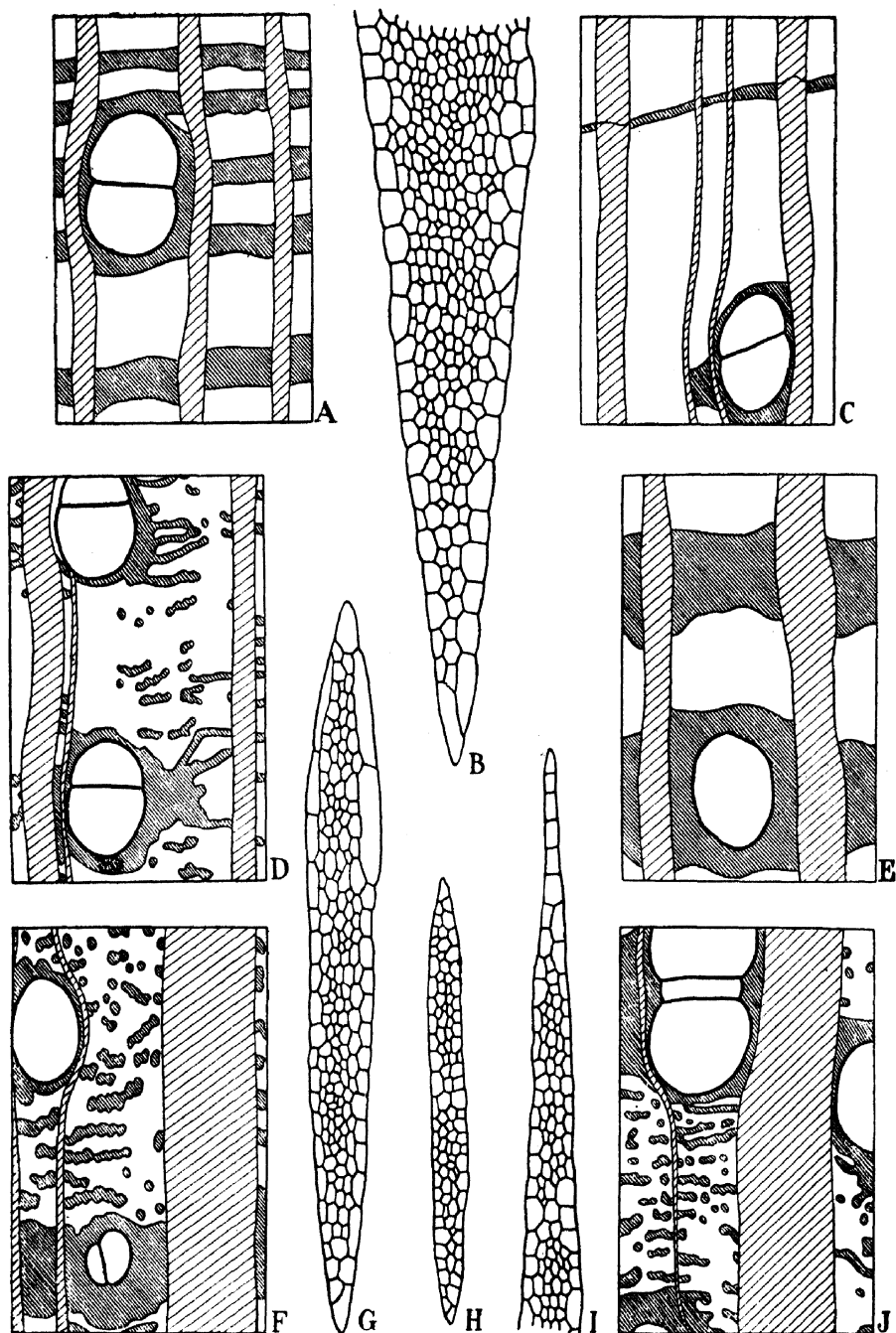


FIG. 61. STERCULIACEAE

A, *Sterculia blancoi* Rolfe. B, '*Pterocymbium javanicum* R.Br.' C, '*Scaphium macropodium* Miq.' D, *Tarrietia simplicifolia* Mast. E, *Cola cordifolia* Sim. F, *Brachychiton acerifolius* F. Muell. G, *Tarrietia utilis* Sprague. H, *Heritiera littoralis* (Dryand.) Ait. I, '*Scaphium macropodium* Miq.' J, *Sterculia carthaginensis* Cav.

strands of thick-walled fibres, mostly developed as caps to the exterior of the phloem groups. Primary medullary rays usually triangular where traversing the phloem, with their broad portions outwardly directed; this character being particularly well defined in certain species of *Fremontia*, *Guazuma*, *Heritiera*, and *Theobroma*. **Phloem** strands also triangular in transverse sections, but with the narrowest portions towards the exterior; more or less distinctly stratified into fibrous and non-fibrous bands in old material. **Xylem** forming a closed cylinder except where interrupted by the relatively broad primary medullary rays. Vessels with simple perforations. **Medullary bundles**, see 'Anomalous Structure'. **Mucilage cavities and cells** (see also 'Leaf') occur in members of all the tribes recognized by Bentham and Hooker, but not in all of the genera and species; situated in the primary cortex and phloem. **Mucilage canals**, partly lysigenous and partly schizogenous in origin, varying in number at different levels in the same plant, arranged in 1 or 2 more or less regular circles in the primary cortex and/or pith. **Fruit stalks** polystelic in certain species of *Helicteres*, *Kleinhovia*, and *Sterculia*.

WOOD¹

(a) *Excluding Buettnerioideae* (Fig. 61)

Vessels mostly medium-sized (100–200 μ mean tangential diameter), large (more than 200 μ) in some species of *Pterocymbium*, *Pterygota*, *Scaphium*, *Sterculia*, and *Tarrietia*, very small in *Octolobus*; solitary and in small radial multiples, the percentage of solitary vessels highest (50–6 per cent.) in the woods with the largest vessels, e.g. *Pterocymbium*, *Sterculia*,² and *Tarrietia*; multiples of 4 or more cells common locally in some woods, e.g. *Heritiera* spp.; 1–5 per sq. mm., except in *Octolobus* (11 per sq. mm.); ring-porous in occasional species of *Firmiana* and *Sterculia* (1851); spiral thickening reported in *Heritiera macrophylla* Wall. (2158) and *Sterculia* p.p. (1851). Perforations simple. Intervascular pitting alternate, never large, small in *Argyrodendron*, *Heritiera*, and *Octolobus*, often with coalescent apertures; pits to ray or wood parenchyma cells similar to the intervacular pitting except in *Brachychiton*, *Firmiana*, and *Sterculia*, in which there are some elongated, simple or slightly bordered pits, with the longer axes often oblique or vertical, and some unilaterally compound pits, e.g. in *Firmiana*. Usually without contents but solid deposits sometimes present in small amounts; tyloses observed only in a single specimen of *Heritiera macrophylla*. Chattaway arranges the genera in the following order according to vessel member length: *Pterocymbium* (mean length 540 μ), *Scaphium*, *Brachychiton*, *Sterculia* A, *Firmiana*, *Tarrietia*, *Argyrodendron*, *Cola*, *Pterygota*, *Sterculia* B, *Heritiera*

¹ Based largely on Chattaway (375).

² Chattaway (375) divides the species of *Sterculia* into the following groups according to their wood anatomy. *Sterculia* A. Metatracheal parenchyma predominantly in lines 1 cell wide: *S. angustifolia* Roxb.; *S. cariboea* R. Br.; *S. carthaginensis* Cav.; *S. columbiana* Sprague; *S. crassiramea* Merril; *S. foetida* L.; *S. harmanda* Pierre; *S. hypochra* Pierre; *S. javanica* R. Br.; *S. macrophylla* Vent.; *S. montana* Merril; *S. oblongata* R. Br.; *S. ornata* Wall.; *S. parviflora* Roxb.; *S. philippinensis* Merril; *S. recordiana* Standl. (Standley 1935); *S. rubiginosa* Vent.; *S. spangleri* R. Br.; *S. tragacantha* Lindl.; *S. urceolata* Smith; *S. villosa* Roxb.

Sterculia B. Metatracheal parenchyma and paratracheal parenchyma often indistinguishable, predominantly in broad bands 3 or 4 cells wide: *S. appendiculata* K. Schum.; *S. blancoi* Rolfe; *S. blumei* G. Don.; *S. cinerea* A. Rich.; *S. coccinea* Roxb.; *S. elegantiflora* Hutch. and Dalz.; *S. oblonga* Mast.; *S. pallens* Wall.; *S. quinqueloba* K. Schum.; *S. rhinopetala* K. Schum.; *S. urens* Roxb.

(370 μ), and single specimens of *Octolobus* and *Eribroma* at about 250 μ . **Parenchyma** abundant; as scattered cells and narrow, uniseriate lines, together with distinct vasicentric sheaths in *Brachychiton* (Fig. 61 F), *Heritiera*, *Pterocymbium*, *Sterculia* A, and *Tarrietia* (Fig. 61 D); in broad bands, 4 or more cells wide, in *Argyrodendron*, *Cola* (Fig. 61 E), *Eribroma*, *Firmiana*, *Octolobus*, *Pterygota*, and *Sterculia* B (Fig. 61 A), the bands sometimes regular and apparently apotracheal together with distinct vasicentric sheaths, sometimes irregular, anastomosing and enclosing all the vessels, particularly in some species of *Firmiana* and *Pterygota*; entirely paratracheal (vasicentric or slightly aliform) in *Scaphium*, the wings sometimes confluent between adjacent vessels or, more rarely, connected with narrow bands; terminal bands present in several species, often rather sporadic in occurrence. Crystals regularly present in *Brachychiton*, *Eribroma*, and *Pterygota*, present in most species of *Argyrodendron*, *Heritiera*, *Sterculia*, and *Tarrietia*, occurring sporadically in *Cola* and not observed in *Firmiana*, *Octolobus*, *Pterocymbium*, and *Scaphium*; silica present in species of *Heritiera* and *Tarrietia* (794); sometimes with dark, gum-like contents. Strands usually of 2 cells in the scattered cells and uniseriate bands, and with some fusiform cells, particularly in some species of *Pterocymbium* and *Sterculia* A, but of 4, occasionally 8, cells in the vasicentric sheaths; strands usually of 4, sometimes 8, cells in the broad bands, though occasionally of only 2 cells on the margins of the bands. Chattaway (375) has shown that broad bands and strands of 4 cells are characteristic of the genera with short vessel members, and narrow bands and strands of 2 cells of the genera with longer vessel members. Distinctly storied. **Rays** often of 2 distinct sizes, e.g. in most species of *Argyrodendron*, *Brachychiton*, *Cola*, *Eribroma*, *Pterocymbium*, *Pterygota*, *Scaphium*, and *Sterculia*; the larger rays 5–10 cells wide in most species of *Heritiera* and *Octolobus* and more than 10 cells wide in most species of *Argyrodendron*, *Brachychiton*, *Eribroma*, *Pterocymbium*, *Pterygota*, *Scaphium*, *Sterculia*, and *Tarrietia* and up to 20 or more cells in some species of *Brachychiton* and *Sterculia* A; varying above and below 10 cells wide in *Cola*, *Firmiana*, and *Tarrietia*; the larger rays more than 1 story high and commonly 1–4 mm. high except in *Heritiera* and some species of *Tarrietia*; uniseriate rays scarce in *Cola* p.p., *Eribroma*, *Octolobus*, *Pterocymbium* p.p., *Pterygota*, and *Sterculia* B; uniseriate rays numerous and storied and multiseriate rays relatively few in *Scaphium*; typically 2–4 rays per mm., but 5–8 per mm. in some species of *Cola*, *Firmiana*, *Heritiera*, *Octolobus*, and *Scaphium*; markedly heterogeneous with 2 to several marginal rows of upright cells (Kribs's Type II A and B) and with sheath cells, except in *Heritiera* and *Octolobus*, in which sheath cells are lacking and in which the multiseriate rays of some species are almost homogeneous and the uniseriate rays contain many procumbent cells. Sometimes with dark gum-like contents; crystals present in at least some species of *Argyrodendron*, *Brachychiton*, *Cola*, *Eribroma*, *Heritiera*, *Pterygota*, *Sterculia*, and *Tarrietia*; silica present in some species of *Heritiera*, *Scaphium*, and *Tarrietia* (794); the small rays storied where sufficiently numerous, e.g. in *Scaphium*. **Fibres** with simple pits that tend to be limited to the middle portion when the fibres are storied; storied in *Argyrodendron*, *Brachychiton*, *Firmiana*, *Pterocymbium*, *Pterygota*, *Scaphium*, *Sterculia* A, and *Tarrietia*. Crystal-bearing fibres are recorded by Chattaway (375) in *Eribroma* and *Sterculia* spp., but Milanez (1526) questions whether

these elements are properly described as fibres. Chattaway (375) discusses the lengths of the fibres in relation to vessel member length; the mean lengths for the genera vary from 1.2 to 2.5 mm. (mostly 1.7–2.0 mm.) and the ratios of fibre length to vessel member length from 3 to 6.5, the higher ratios being typical of the genera with the shortest vessel member lengths. **Intercellular canals** of the vertical traumatic type observed in occasional specimens of *Brachychiton* and *Heritiera* and also reported by Record (1787) in *Sterculia* and *Tarrietia* and by den Berger (182) in *Firmiana*, *Pterocymbium*, and *Scaphium*. **Anomalous structure.** In *Brachychiton rupestris* K. Schum., the 'Australian bottle tree', the xylem is separated into thin layers by wide sheaths of parenchyma containing large empty cavities, which are possibly connected with the storage of water.

Besson (186) shows a rather high percentage of silica in the ash of *Tarrietia cochinchinensis* Pierre and a very high percentage (65.85) in *Cola attiensis* Aubrév. et Pellegr.

(b) *Buettnerioideae* (Fig. 62)

Vessels mostly medium-sized (100–200 μ mean tangential diameter), slightly larger in some species of *Pterospermum* and in *Triplochiton*, moderately small (50–100 μ) in some species of *Reevesia*, *Scaphopetalum*, and *Theobroma*, very small (25–50 μ) in *Helicteres*, *Leptonychia*, *Mansonia gagei* Drummond, and *Waltheria*; solitary and in small multiples and clusters, multiples of 2 or 3 cells very common in some of the genera, multiples of 4 or more cells common in *Dombeya* p.p., *Eriolaena* p.p., *Helicteres*, *Kleinhovia* p.p., and *Leptonychia* and tending to be abundant in localized zones in several other genera; in large groups of very small vessels in *Fremontia* (Fig. 62 j) and most species of *Reevesia*,¹ the groups tending to produce an oblique or tangential pattern; mostly 5–20 per sq. mm., 1–5 per sq. mm. in *Cheirostemon*, *Guazuma*, *Pterospermum*, *Theobroma* p.p., and *Triplochiton*, 50–75 per sq. mm. in *Helicteres*, *Mansonia gagei*, and *Waltheria*, and too numerous to count in *Fremontia* and *Reevesia*;¹ semi-ring-porous or ring-porous in some species of *Fremontia*, *Helicteres*, *Kleinhovia*, and *Reevesia*;¹ with spiral thickening in *Fremontia* and *Reevesia*.¹ Perforations simple. Intervascular pitting alternate, rather small, sometimes minute, e.g. in *Dombeya*, *Helicteres*, *Mansonia*, and *Pterospermum*, moderately large and occasionally elliptical in *Cheirostemon* and *Theobroma*; pits to ray and wood parenchyma similar to the intervacular pitting. Usually without contents, but solid deposits present in small amounts in *Mansonia gagei* and *Scaphopetalum*; tyloses observed only in *Eriolaena spectabilis* Planch. and *Triplochiton*. Mean member length 0.2–0.4 mm. **Parenchyma** often abundant; most typically as scattered cells, or numerous short uniseriate lines alternating with 1–3 rows of fibres (Fig. 62 A and D), together with distinct sheaths round the vessels, except in *Reevesia*;¹ entirely or predominantly paratracheal, as vasicentric, aliform, or locally confluent sheaths round the vessels (Fig. 62 c and G), in *Dombeya*, *Eriolaena*, *Helicteres* p.p., *Melochia*, and *Waltheria*. Crystals, either in chambered or ordinary cells, and gummy deposits present in a few species, but usually absent from the parenchyma cells even though abundant in the rays. Strands typically of 4 cells; strands of 2 cells common or predominant in *Dombeya* p.p., *Eriolaena*,

¹ Except *Reevesia wallichii* R. Br.

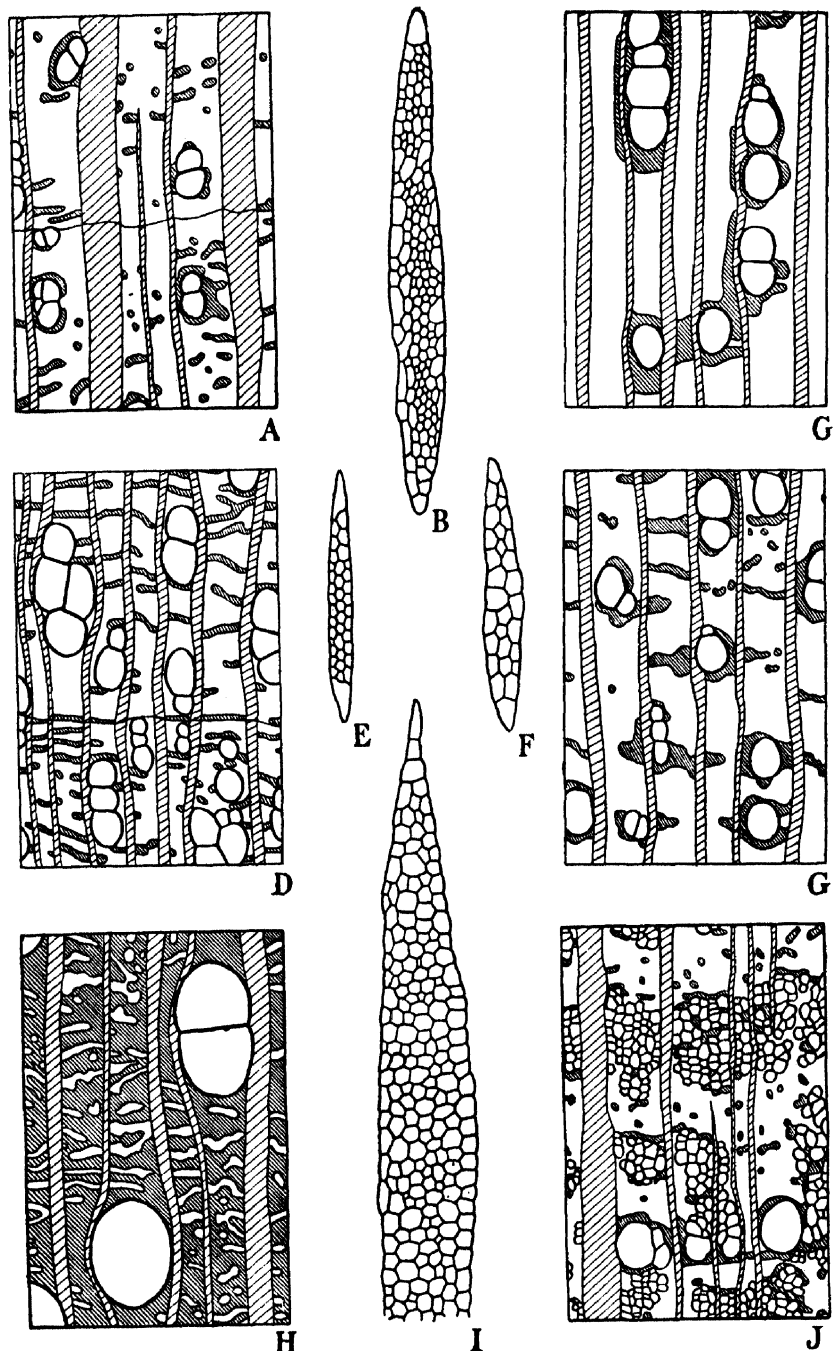


FIG. 62. STERCULIACEAE-BUETTNERIOIDEAE

A, *Theobroma cacao* Linn. B, *Triplochiton scleroxylon* K. Schum. C, *Dombeya mastersii* Hook. f. D, *Mansonia altissima* A. Chev. E, *M. altissima* A. Chev. F, *Eriolaena stocksii* Hook. f. et Thoms. G, *E. stocksii* Hook. f. et Thoms. H, *Triplochiton scleroxylon* K. Schum. I, *Theobroma cacao* Linn. J, *Fremontia californica* Torr.

Fremontia, and *Triplochiton*, and of 6–8 cells in *Leptonychia*; fusiform cells common in some species of *Dombeya*, *Eriolaena*, and *Triplochiton*. Distinctly storied, except in *Commersonia*, *Fremontia*, *Helicteres*, *Leptonychia*, *Melochia*, *Pterospermum* p.p., and *Waltheria*. **Rays** of 2 distinct sizes in *Cheirostemon*, *Leptonychia*, *Pterospermum* p.p., *Reevesia* p.p., *Scaphopetalum*, and *Theobroma*; the larger rays mostly 4–7 cells wide; 2–3 cells wide in *Eriolaena*, *Helicteres*, *Mansonia*, and *Pterospermum* p.p., 8–10 cells wide in *Cheirostemon*, *Fremontia*, *Reevesia*,¹ and *Theobroma* p.p. and up to 20 cells wide in some species of *Theobroma*; the larger rays typically more than 1 story high, except in *Mansonia* and a few species of *Pterospermum*, more than 1 mm. high in *Cheirostemon*, *Commersonia*, *Guazuma*, *Leptonychia*, *Melochia* p.p., *Pterospermum* p.p., *Reevesia*,¹ and *Scaphopetalum*, and often showing evidence of dissection into smaller units; uniseriate rays numerous, except in *Eriolaena* p.p., *Guazuma*, and *Mansonia*, and very low, often of only 1 or 2 cells, in *Fremontia*; most commonly 4–12 rays per mm., but 13–20 per mm. in *Helicteres*, *Kleinhovia* p.p., *Leptonychia*, *Pterospermum* p.p., *Scaphopetalum*, a few species of *Theobroma*, and *Waltheria*; typically distinctly heterogeneous, with 2–4 marginal rows of upright cells and heterogeneous uniseriate rays (Kribs's Type II B), with more numerous marginal rows and uniseriates of upright cells only (Kribs's Type II A) in *Scaphopetalum*, verging on homogeneous in some species of *Dombeya* and *Mansonia*; with sheath cells in *Cheirostemon*, *Commersonia*, *Fremontia*, *Leptonychia*, *Melochia* p.p., *Reevesia wallichii* R. Br., *Scaphopetalum*, and *Theobroma* p.p. Sometimes with dark gum-like contents; crystals observed in at least some species of *Commersonia*, *Fremontia*, *Helicteres*, *Kleinhovia*, *Leptonychia*, *Mansonia*, *Pterospermum*, *Scaphopetalum*, *Theobroma*, and *Triplochiton*, rays nearly all short and prominently storied in *Dombeya* p.p., *Kleinhovia*, *Mansonia*, and *Pterospermum* p.p., with only the smaller rays storied in some species of *Dombeya*, *Eriolaena*, *Helicteres*, *Pterospermum*, *Reevesia*, and *Theobroma*. **Tile cells** of the 'Durio' type (372) present in *Guazuma*, *Kleinhovia*, *Leptonychia*, and *Scaphopetalum*, and of the 'Pterospermum' type in *Melochia* p.p. and *Pterospermum*, and intermediate between the 2 types in *Reevesia* and *Triplochiton*. **Fibres** with small simple pits, sometimes markedly more numerous on the radial than on the tangential walls and varying from few to numerous. With plugs of gum and very occasional septa in *Eriolaena*. Walls usually rather thin, very thin in some species of *Melochia* and *Theobroma*, thick in *Eriolaena*, *Fremontia*, *Hibiscus*, and *Mansonia*. Moderately distinctly storied in *Cheirostemon*, *Guazuma*, *Kleinhovia*, and *Mansonia* and rather vaguely storied in some other genera. Mean length 1.0–1.7 mm. **Intercellular canals** of the vertical traumatic type reported by Record (1787) in *Theobroma*.

ROOT

Root generally containing **mucilage cells** and cavities (but not canals), situated in the primary cortex as well as in the rays where passing through the phloem. Mucilage receptacles stated to be absent from certain species of *Cheiranthodendron*, *Dombeya*, *Heritiera*, *Pterospermum*, and *Theobroma*. **Buttress roots** with very excentric structure, recorded and described by Francis (707) in a variety of *Tarrietia argyrodendron* Benth. Peg-like **pneu-**

¹ Except *Reevesia wallichii* R. Br.

matophores, arising as localized wings from the horizontal roots and often coalescing with the buttress roots, described by Groom and Wilson (827) for *Heritiera*. The wood of the pneumatophores contains fewer vessels and fibres than normal roots, the tissues being largely parenchymatous and often filled with abundant starch. **Lenticels** present on the surface of the pneumatophores; intercellular spaces also well developed.

ANOMALOUS STRUCTURE

Medullary bundles, with centrally directed phloem, recorded by Solereder and by Pfeiffer (1712) in *Leptonychia* sp.

TAXONOMIC NOTES

(i) BASED ON GENERAL ANATOMY

The resemblance in anatomical characters between the Bombacaceae, Malvaceae, and Sterculiaceae indicates that these families are all closely related to one another. The arc-shaped vascular strand, with incurved ends, which occurs in the petiole of *Fremontia mexicana* Macbride is a very much simpler type than is to be found in most members of the Sterculiaceae. This suggests that *Fremontia* may be rather remotely related to the other genera.

Dehay's (558, 559) investigations concerning the petiolar vascular structure raise problems of considerable interest to phylogenists. He shows that the tribes cannot be arranged in a phylogenetic sequence based on petiolar structure, nor does increasing complexity of petiolar structure run parallel to corresponding stages in floral evolution. Dehay's work fully confirms the close affinities between the Sterculiaceae and Tiliaceae.

(ii) BASED ON WOOD STRUCTURE

Chattaway (375) states that the anatomical evidence supports the conclusion of Edlin (622) that the family name Sterculiaceae should be restricted to the Sterculieae. Discussing the taxonomic position of the genera within the family, Chattaway makes the following suggestions: *Sterculia pallens* Wall. to be transferred to *Firmiana*, *Brachychiton* and *Eriobroma* to be again sunk in *Sterculia*, and the genus *Sterculia* to be subdivided into 2 sub-genera.

The woods which have here been described under Sterculiaceae-Buettnerioideae, and which some botanists treat as a distinct family the Buettneriaceae, fall into 2 fairly distinct groups according to their parenchyma, as follows:

- (a) Parenchyma predominantly apotracheal (diffuse) in Edlin's 'Buettnerieae, Helicteraeae, and Mansonieae.
- (b) Parenchyma exclusively paratracheal (vasicentric to aliform) in Edlin's Dombeyeae, Eriolaeneae, and Hermannieae.

Tile cells follow much the same grouping as above, being commonly present in Edlin's Buettnerieae, but absent from Dombeyeae and Eriolaeneae, and rare in Hermannieae.

Reevesia wallichii R. Br. differs markedly from *R. cavaleriei* Léveillé et Variot and *R. pubescens* Mast., though the differences might conceivably be due to habitat. *Cistanthera* is very similar to *Mansonia*, and would fit easily in the Buettnerioideae. *Cheirostemon* would fit better in the Bombacoideae (but not in the Durioneae). *Fremontia* is exceptional, with ulmiform vessels, spiral

thickening, and almost homogeneous, wide and high rays. This type of vessel does occur in *Reevesia* p.p. but is more common in the Malvaceae, e.g. *Malva-viscus*. The parenchyma would fit the Bombacaceae but other features less well. Edlin's grouping of *Fremontia* with *Cheirostemon* at first sight seems improbable, but the chief differences are of the same nature as those that distinguish the different species of *Reevesia*.

ECONOMIC USES

Fibre is obtained from the inner bark of various members of the family. Gums are obtained from several species of *Sterculia*. Kola nuts, used as substitutes for tea and coffee, are the dried seeds of *Cola vera* K. Schum. Cocoa consists of the specially prepared seeds of *Theobroma cacao* Linn.

The timbers of this family vary from soft, coarse, and perishable to hard, heavy, and durable. None of the timbers derived from the Sterculiaceae *sensu stricto* is of first-class importance, though two of the genera, *Heritiera* and *Tarrietia*, are of some importance locally; the wood of *Heritiera fomes* Buch. affords an example of the heavy, durable type of wood and is extensively used in India for boat-building, wheel spokes and felloes, tool-handles, &c., and species of *Tarrietia* from Australia (the 'Tulip Oaks') and West Africa (Niangon) are the source of timbers suitable for cabinet-work, panelling, &c.; some of the lighter woods, such as *Sterculia* spp., furnish packing-case timbers. The Buettnerioideae furnish two timbers of more than local importance, both of them from West Africa; Obeche, Ayous, or Samba (*Triplochiton scleroxylon* K. Schum.) has been widely used for plywood and other purposes, and *Mansonia* or Pruno (*Mansonia altissima* A. Chev.) is a walnut-like joinery timber.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abroma, Cheiranthodendron, Cheirolaena, Cola,* Commersonia, Dombeya,* Fremontia,* Guazuma,* Helicteres, Heritiera,* Hermannia, Hua, Kleinhovia, Lasiopetalum, Leptonychia, Lysiosepalum, Melhania, Pterospermum, Pterygota, Reevesia, Rulingia, Scaphopetalum, Sterculia, Tarrietia, Theobroma,* Trochetia,* Ungeria.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

A. *Excluding Buettnerioideae*

Argyrodendron, Brachychiton, Cola, Eribroma, Firmiana, Heritiera, Octolobus, Pterocymbium, Pterygota, Scaphium, Sterculia, Tarrietia.

B. *Buettnerioideae*

Cheirostemon, Commersonia, Dombeya, Eriolaena, Fremontia, Guazuma, Helicteres, Kleinhovia, Leptonychia, Mansonia, Melochia, Pterospermum, Reevesia, Scaphopetalum, Theobroma, Triplochiton, Waltheria.

LITERATURE

(i) *On General Anatomy*

Dehay 558, 559, Francis 707, Gehrig 753, Groom and Wilson 827, Kienholz 1236, Pfeiffer 1712, Sabnis 1977, Shelton 2086, Zebe 2504.

(ii) *On Wood Structure*

A. *Excluding Buettnerioideae*. Aubréville 51, 52, Baker 104, Benoist 169, den Berger 182, Besson 186, Chattaway 370, 371, 372, 375, Cooper and Record 461, Coster 481, Dadswell 525, Dadswell and Record 533, Dixon 592, Edlin 622, Foxworthy 705, Giordano 786, Gonggrijp 794, Howard 1088, Isenberg 1124, Janssonius 1154, Jentsch 1174, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Leon 1359, Link 1377, Méniard 1492, Milanez 1526, Panshin 1649, Pearson and Brown 1679, Record 1781, 1783, 1801, 1809, 1824, 1843, 1851, 1871, 1885, Record and Hess 1886, Record and Mell 1894, Ridley 1935, Swain 2224, Tang 2231, Torres 2269, Tupper 2295, Williams 2430.

B. *Buettnerioideae*. Aubréville 52, Beekman 167, den Berger 179, 182, Besson 186, Chattaway 371, 372, 375, Cooper and Record 461, Cozzo 494, Dadswell and Record 533, Edlin 622, Howard 1088, Janssonius 1154, Jentsch 1172, Kanehira 1206, Lecomte 1334, Méniard 1491, Metcalfe 1496, Ortega 1641, Pearson and Brown 1679, Record 1781, 1787, 1801, 1809, 1818, 1823, 1829, 1843, 1851, 1871, 1872, 1873, 1874, Record and Hess 1886, Record and Mell 1894, Stone 2206, Tang 2231, Tupper 2295, Williams 2430.

66. TILIACEAE

(FIG. 60 on p. 244; FIG. 63 on p. 256)

SUMMARY

(i) GENERAL

A world-wide family consisting mainly of trees and shrubs, but including a few herbs. The family has many anatomical features in common with the Bombacaceae, Malvaceae, and Sterculiaceae. **Mucilage** is present in **cells**, **cavities**, or, more rarely, **canals** in the cortex and/or pith of the stem as well as in the cortex of the petiole and sometimes in the leaf lamina. The **stomata** are ranunculaceous. **Veins** are embedded in the mesophyll; sometimes vertically transcurrent. The vascular structure of the **petiole** is very variable, ranging from a single arc-shaped strand to cylindrical types enclosing 1 or more medullary bundles. The **cork** arises in the sub-epidermis of the young stem; the **cortex** often contains an outer collenchymatous and an inner parenchymatous zone. In the **pericycle** there are usually well-developed strands of fibres, situated externally to the phloem. Transverse sections nearly always show the **phloem** as triangular strands with the apices outwardly directed, and stratified into fibrous and non-fibrous portions.

(ii) WOOD

Vessels small to medium-sized, with radial multiples of 4, or more, cells in some genera, semi-ring-porous and with spiral thickening in a few species; perforations simple, intervacular pitting minute to moderately large, pits to ray and wood parenchyma similar to the intervacular pitting or elongated and simple; members of medium length to moderately short. **Parenchyma** predominantly apotracheal, in numerous, short, irregular, uniseriate bands, but predominantly paratracheal—vasicentric to aliform—in some genera and intermediate between apotracheal and paratracheal in others; often storied. **Rays** (a) in the Brownlowiaceae, 2–3 cells wide, with few uniseriates, short and storied, (b) in the other genera, typically, but with some exceptions, of 2 sizes, with numerous uniseriates that tend to be storied, and high, unstoried rays 4–15 cells wide; sheath cells and tile cells present in several genera. **Fibres** with numerous simple pits, frequently storied; very short to moderately long, but mostly of medium length.

LEAF

Generally dorsiventral, but consisting wholly of palisade tissue in certain species of *Apeiba*, *Berrya*, *Corchorus*, *Diplodiscus*, *Grewia*, as well as in other genera especially amongst the Brownlowieae. **Hairs** unicellular, uniseriate, stellate, tufted, peltate, and glandular. Specially long, unicellular hairs recorded by Gehrig (753) in *Sparmannia africana* Linn. Peltate scales recorded in species of *Brownlowia*, *Diplodiscus*, *Mollia*, *Pentace*, but probably present in other genera as well. **Stomata** generally confined to the lower surface (recorded on the upper surface in species of *Corchorus*); usually ranunculaceous. A **xerophytic form** of *Tilia glabra* Vent. described by Starr (2188) as differing from a mesophytic form of the same species in having (i) the upper epidermal cells less tall, but larger in surface area and divided periclinally; (ii) palisade cells taller, sometimes tending to be in 2 layers. **Midrib** of *Tilia* always including some sclerenchyma according to Gehrig (753). Vascular structure of the **petiole** very variable, its transverse appearance ranging from a single arc-shaped strand to cylindrical types enclosing 1 or more subsidiary bundles in the pith. Petiolar vascular strand arc-shaped in species of *Corchorus* (Fig. 60 j) and *Grewia vernicosa* Schinz; arc-shaped but with accessory bundles within the arc in *Glyphaea grewioides* Hook. f.; in the form of an almost or completely closed ring in *Berrya ammonilla* Roxb. and *Grewia* sp.; in the form of a closed ring surrounding a complex of medullary bundles in *Tilia* spp. (Fig. 60 i). Dehay's (560) recent investigations on the petiolar structure of the Tiliaceae confirm and extend the foregoing records based on material examined at Kew. Dehay records, in transverse sections through the distal end, a simple crescentic vascular strand in *Corchorus*, *Sparmannia*, and *Triumfetta*, but with vestiges of a more complex structure in certain species of *Sparmannia* and *Triumfetta*; an almost closed vascular ring surrounding a medullary strand in *Berrya* and *Tilia*; a vascular ring with the adaxial part very strongly invaginated, and dissected into separate strands situated close to the bundles of the medullary system in *Brownlowia* and *Columbia*, whilst actual fusion between the adaxial part of the ring and the medullary bundles was observed in *Columbia scabra* A. DC. **Mucilage cells** recorded in the epidermis of *Desplatzia suberica* Bocq. and *Glyphaea grewioides* Hook. f. Mucilage cells or spaces common in the mesophyll. **Mucilage canals** recorded by Coverlid (489) in the abaxial side of the midrib and near the upper surface of the leaf in *Grewia polygama* Willd. Petiole also containing mucilage cells or cavities, the latter often considerably elongated, situated in the 'cortex' and/or 'pith' of most genera. **Crystals** common; mostly clustered, but sometimes solitary; in some species most numerous around the vascular bundles.

AXIS

YOUNG STEM (Fig. 60 k and m)

Cork sub-epidermal in origin; cells with fairly thin walls and strongly compressed in a radial direction in *Tilia*; cells sclerotic in *Apeiba* and *Vasivaea*. **Cortex** containing parenchymatous and collenchymatous zones. **Pericycle** generally including groups of fibres situated externally to the phloem. **Phloem** most commonly as triangular strands with the narrowest portions

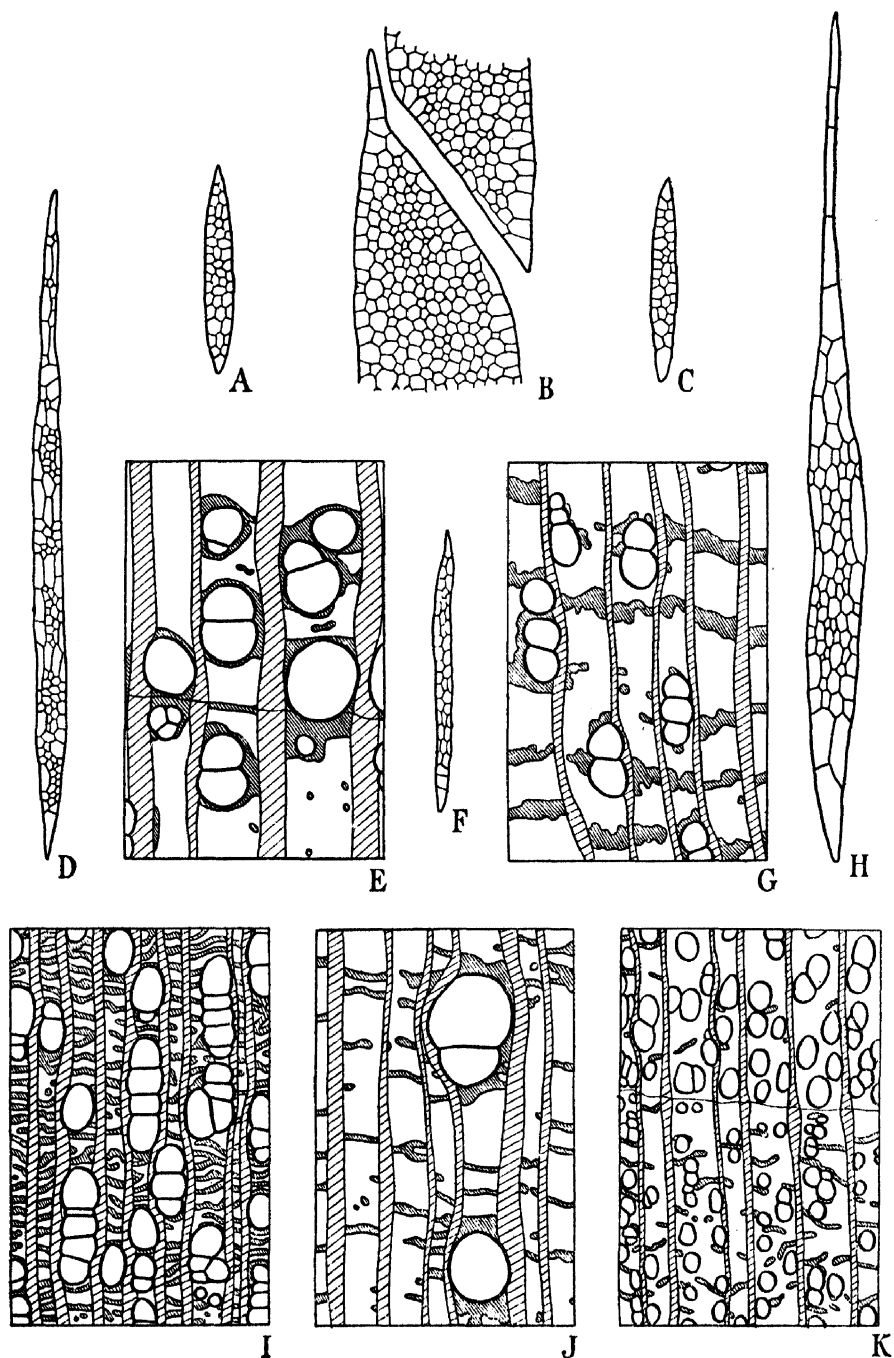


FIG. 63. *TILIACEAE*

A, *Cistanthera papaverifera* A. Chev. B, *Columbia floribunda* Kurz. C, *Pentace burmanica* Kurz. D, *Grewia excelsa* Vahl. E, *G. mollis* A. Juss. F, *Tilia vulgaris* Hayne. G, *Christiana africana* DC. H, *Heliocarpus popayanensis* H. B. et K. I, *Cistanthera papaverifera* A. Chev. J, *Lueheopsis flavescens* (Britt.) Burret. K, *Tilia cordata* Mill.

towards the exterior, separated by the wide distal ends of the primary medullary rays with their broadest portions towards the exterior (cf. *Bombacaceae*, *Malvaceae*, and *Sterculiaceae*). **Xylem** in the form of a more or less closed cylinder, but locally traversed by rather broad medullary rays. Interruptions in the xylem ring much broader and more conspicuous in some genera and species than in the others. Vessels with simple perforations. **Mucilage** usually present in **cells** or **cavities** situated in the cortex phloem and/or pith. Scattered, presumably tanniniferous cells, with contents readily stained with haematoxylin, common in the parenchymatous tissues. Solitary and clustered **crystals** of calcium oxalate common. Large, elongated prismatic crystals resembling styloids abundant in the bark of *Tilia*. '**Adventitious stemlets**' have been described by Richter (1934) arising from a stem of *Tilia cordata* Mill. which had been damaged by lightning.

WOOD (Fig. 63)

Vessels mostly medium-sized (100–200 μ tangential diameter), moderately small (50–100 μ), in some species of *Berrya*, *Brownlowia*, *Carpodiptera*, *Christiana*, *Cistanthera*, *Desplatzia*, *Entelea* (1295), *Glyphaea*, *Microcos*, *Pityranthe*, *Schouteria* (1154), *Sparmannia*, *Tilia*, *Triumfetta*, *Vallea*, and *Vinticina* (1295); with multiples of four or more cells few to moderately common in *Brownlowia*, *Carpodiptera*, *Christiana*, *Cistanthera*, *Heliocarpus*, *Luehea*, *Microcos*, *Pentace*, and *Pityranthe*; irregular clusters sometimes locally abundant in *Brownlowia*, *Columbia*, and *Heliocarpus*; commonly 6–20 per sq. mm., fewer than 5 per sq. mm. in some species of *Althoffia* (1295), *Apeiba*, *Belotia*, *Brownlowia*, *Entelea* (1295), *Goethalsia*, *Heliocarpus*, *Luehea*, *Lueheopsis*, *Microcos*, *Mortoniendendron*, *Pentace*, and *Trichospermum*, 20–40 per sq. mm. in *Cistanthera*, *Pityranthe*, *Sparmannia*, and *Triumfetta* p.p.; 40–70 per sq. mm. in *Tilia* and *Triumfetta* p.p.; semi-ring-porous in some species of *Erinocarpus* and *Grewia*; with spiral thickening in *Luehea seemmannii* Pl. et Tr. and *Tilia*, and in the smaller vessels of *Chartocalyx* (1295). Perforations simple. Intervascular pitting commonly small to minute, sometimes extremely small, e.g. in *Diplodiscus*, *Glyphaea*, *Mollia*, and *Mortoniendendron* (1886), tending to be less small in the *Grewieae*, e.g. *Columbia*, *Desplatzia*, *Duboscia*, *Erinocarpus*, and *Triumfetta*, and moderately large to large in *Belotia*, *Heliocarpus*, *Sparmannia*, and *Trichospermum*; alternate, rather rarely with coalescent apertures; pits to ray and wood parenchyma usually similar to the intervacular pitting but with some simple, larger, and elongated pits, and, according to Kukachka and Rees (1295), often unilaterally compound in most of the *Brownlowieae*, e.g. *Berrya*, *Brownlowia*, *Carpodiptera*, *Diplodiscus*, and *Pentace*, and also in *Erinocarpus*, *Heliocarpus*, *Sparmannia*, *Triumfetta*, and *Trichospermum*; also, according to Kukachka and Rees (1295), in *Glyphaea*; simple, without being larger, in a few genera, e.g. *Belotia*. Sometimes with abundant gummy deposits, e.g. *Actinophora*, *Carpodiptera*, *Cistanthera*, *Duboscia*, and *Pentace*; tyloses observed in *Berrya*, *Carpodiptera*, *Christiana*, *Grewia*, *Heliocarpus*, and *Pentace*. Mean member length 0.26–0.7 mm., mostly 0.35–0.45 mm.; shortest in *Carpodiptera*, *Chartocalyx*, *Grewia* p.p., and *Vinticina* (1295). **Parenchyma** usually moderately abundant, (a) predominantly apotracheal, in irregular, short, numerous, uniseriate bands (Fig. 63 i and k) in *Actinophora*, *Apeiba*, *Brownlowia*, *Cistanthera*, *Columbia*, *Desplatzia*, *Diplodiscus*,

Duboscia, *Goethalsia*, *Heliocarpus* p.p., *Luehea*, *Luehopsis* p.p., *Microcos*, *Pentace*, *Schoutenia* p.p. (1154), *Tilia*, and *Trichospermum*, often with some vasicentric parenchyma in addition, particularly in *Apeiba*, *Diplodiscus*, *Grewia*, *Heliocarpus*, *Luehea*, *Pentace*, and *Trichospermum*; in more regular bands 1–2 cells wide in some species of *Luehopsis* (Fig. 63 J); (b) predominantly paratracheal—vasicentric to aliform—with or without a little diffuse parenchyma in *Belotia* (diffuse abundant in some species, 1295), *Erinocarpus*, *Grewia* (Fig. 63 E), *Heliocarpus* p.p., *Mollia*, *Pityranthe*, *Schoutenia* p.p. (1154), *Sparmannia*, *Triumfetta*, and *Vinticina* (1295). Intermediate forms occur in some genera, e.g. aliform mixed with irregular apotracheal bands and scattered cells in *Carpodiptera* and *Christiana* (Fig. 63 G) and aliform with occasional broad, possibly confluent bands in *Berrya* and *Pityranthe*. Terminal bands usually present. The woods of *Apeiba*, *Entelea*, *Heliocarpus*, *Sparmannia*, and *Triumfetta* are characterized by the occurrence of an unusual form of pith-like parenchyma, with very thin walls and few contents, in addition to the common types. In cross-section this parenchyma appears as islands (comparable with included phloem of the 'Strychnos' type), as bands of varying width (up to $\frac{1}{8}$ in. in *Apeiba*) or as both. The cells are elongated radially in *Apeiba* and, to a less extent, in *Entelea* (1295). Chambered crystals present in a few genera, e.g. *Cistanthera*, *Erinocarpus*, *Grewia*, *Heliocarpus*, and *Lueheopsis*; dark gummy contents abundant in some species. Silica bodies have been observed in *Brownlowia* sp. (2158). Strands usually predominantly of 4 or 8 cells, strands of 2 cells common in only a few species; with some fusiform cells in *Erinocarpus* and *Grewia celtidifolia* Juss. (1154). Storied in *Apeiba*, *Belotia*, *Berrya*, *Brownlowia*, *Carpodiptera*, *Christiana*, *Cistanthera*, *Columbia*, *Diplodiscus*, *Erinocarpus*, *Goethalsia*, *Grewia*, *Heliocarpus*, *Luehea*, *Lueheopsis*, *Mollia*, *Pentace*, *Pityranthe*, *Schoutenia* (1295), *Tilia*, and *Vinticina* (1295). **Rays** (a) in the Brownlowieae (Fig. 63 C), e.g. *Berrya*, *Brownlowia*, *Carpodiptera*, *Christiana*, *Diplodiscus*, *Pentace*, and *Pityranthe*—typically 2–3 cells wide, but up to 4–5 cells in some species of *Pentace* and *Pityranthe*; largest rays less than 1 mm. high and seldom more than 1 story high; uniseriate rays scarce; 6–12 rays per mm.; heterogeneous (Kribs's Type II B), with 1 or 2 marginal rows of square or upright cells to almost homogeneous (Type I); frequently containing dark gummy contents and crystals in the upright or procumbent cells; all the rays regularly storied. In *Diplodiscus* the rays are similar in width, but differ in several other respects, e.g. the uniseriate rays are common, composed almost entirely of procumbent cells, often more than 1 story high and only vaguely storied; the multiseriate rays are high (up to 2 mm.), not storied and almost homogeneous. (b) In the other tribes commonly of 2 distinct sizes, with numerous uniseriate rays; the larger rays 4–9 cells wide in most of the genera, 10 or more cells wide in *Columbia*, *Duboscia*, and *Sparmannia*, and 3 cells wide in *Cistanthera*; typically more than 1 story and more than 1 mm. high, though slightly less than 1 mm. in some species of *Desplatzia* and *Microcos* and showing evidence of dissection into smaller units in *Columbia* (Fig. 63 B) and *Heliocarpus* p.p.; rays all short and storied in *Cistanthera* and *Luehea*; most commonly 11–20 per mm. but sometimes fewer (8–10 per mm.) in *Columbia*, *Erinocarpus*, *Heliocarpus*, *Lueheopsis*, *Microcos*, *Sparmannia*, *Tilia*, *Triumfetta*, and *Trichospermum*, and 4–7 per mm. in *Mortoniodendron* and *Tilia*, p.p.; typically heterogeneous

(Kribs's Type II A and B); with 4 or more marginal rows of square or upright cells in *Althoffia* (1295), *Apeiba*, *Belotia*, *Desplatzia* p.p., *Erinocarpus*, *Glyphaea*, *Heliocarpus* p.p. (Fig. 63 H), *Lueheopsis* p.p., *Microcos*, *Mollia*, and *Sparmannia*, and with 10 or more rows in *Duboscia*, *Heliocarpus* p.p., *Trichospermum*, and *Triumfetta*; sometimes homogeneous (Kribs's Type I) in *Tilia* and some specimens of *Cistanthera papaverifera* A. Chev.; sheath cells present on *Althoffia* (1295), *Entelea* (1295), *Erinocarpus*, *Goethalsia*, *Grewia*, *Heliocarpus*, *Luehea*, *Lueheopsis*, *Mortoniendendron*, *Trichospermum*, *Triumfetta*, and *Vinticina* (1295); tile cells of the 'Durio' type (372) present in *Columbia*, *Desplatzia*, *Grewiopsis* (1295), *Luehea*, *Lueheopsis*, *Mollia*, *Mortoniendendron*, and *Vinticina* (1295), and of the 'Pterospermum' type (372) in *Belotia*,¹ *Duboscia*, *Grewia* (Fig. 63 D), *Mortoniendendron*, and *Trichospermum*, and possibly also in *Sparmannia* and *Triumfetta*, in which the large rays are composed almost entirely of upright cells but with occasional procumbent cells scattered among them. Crystals present in most of the species, sometimes abundant; gummy contents common in the procumbent cells. Nearly all the rays storied in *Cistanthera* and *Luehea* p.p. and, according to Record (1894), in *Diplodiscus*; the smaller rays storied in *Apeiba*, *Belotia*, *Carpodiptera*, *Columbia*, *Diplodiscus*, *Duboscia*, *Goethalsia*, *Grewia*, *Heliocarpus*, *Lueheopsis*, *Mollia*, *Schoutenia* (1154), *Tilia* p.p., *Trichospermum* p.p., and *Vinticina* (1295). **Fibres** typically with numerous slit-like simple pits on the radial walls and relatively few on the tangential walls; less numerous in a few genera, e.g. *Pentace* and *Tilia*, and with small borders in *Tilia*; often with trumpet-shaped canals, the inner aperture sometimes resembling a small border when seen in surface view. With gum-plates in *Berrya*. Walls thick in *Actinophora*, *Brownlowia*, *Carpodiptera*, *Christiana*, *Erinocarpus*, *Grewia* p.p., *Lueheopsis*, *Microcos* p.p., *Pentace* p.p., and *Pityranthe*, and thin in *Apeiba*, *Belotia* p.p., *Duboscia*, *Goethalsia*, *Heliocarpus*, *Microcos* p.p., *Trichospermum*, and *Triumfetta*. Storied, though sometimes rather indistinctly, in the species with storied parenchyma. Deposits of calcium carbonate are reported by Record (1818) in callus tissue of *Tilia americana* L. Mean length 0.8–1.6 mm. (1295). Hyde (1117) refers to the occurrence of a few short fibre-tracheids around the vessels in *Heliocarpus*, and Kukachka and Rees (1295) to **vascular tracheids** in *Erinocarpus* and *Vinticina*. Large, widely separated radial channels occur in *Heliocarpus* and, according to Record and Hess (1886), are present in all species.

GENUS OF UNCERTAIN AFFINITIES. NESOGORDONIA

(The following information is based on Beauvisage's (163) description of *N. bernieri* Baill.)

SUMMARY

A tree with thick leaves, native of Madagascar.

LEAF

Dorsiventral. **Cuticle** thick on the upper surface. **Mesophyll** composed of about 3 layers of short palisade cells and a broad region of spongy tissue. Outer part of the cortical region of the **petiole** collenchymatous, inner part

¹ Kukachka and Rees (1295) describe the tile cells in *Belotia* as of the 'Durio' type.

composed of somewhat spongy parenchyma. Pericyclic region containing bundles of fibres. Petiole supplied by a closed vascular strand with an accessory medullary bundle except at the distal end where the almost annular strand is adaxially concave with inwardly directed ends. **Mucilage cells** present in the epidermis, mesophyll and cortical region of the petiole. Cluster **crystals** also occur.

AXIS

YOUNG STEM

Cortex collenchymatous opposite the bundles of fibres in the pericycle. **Pericycle** containing a ring composed of alternating groups of fibres and parenchyma. **Phloem** strands and distal endings of the primary medullary rays triangular, the phloem being stratified into fibrous and non-fibrous portions. **Xylem** with vessels isolated or in radial rows of 2-5, 20-45 μ in diameter; perforations simple, oblique. Wood fibres composed of radial rows of very thick-walled elements. Rays numerous, 1-3 cells wide. **Pith** composed of lignified pitted cells, not much thickened. Elongated **mucilage cells** present in the cortex and solitary and cluster **crystals** in the cortex and pith.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Tiliaceae constitute an anatomically homogeneous family having undoubted affinities with the Bombacaceae, Malvaceae, and Sterculiaceae. Genera like *Aristotelia*, *Elaeocarpus*, and *Tricuspidaria* are sufficiently distinct from the Tiliaceae to be treated as a separate family, the Elaeocarpaceae. *Hasseltia*, *Plagiopteron*, and *Prockia*, although included in the Tiliaceae in the Bentham and Hooker system, are here treated as members of the Flacourtiaceae, to which they seem to be anatomically more similar. This is also the position to which they have been assigned in the system of Engler and Prantl. *Nesogordonia*, whose taxonomic affinities have been much disputed, exhibits many characters in common with the Tiliaceae, as has already been pointed out by Beauvisage (163). Dehay (560) has drawn attention to the similarity of the petiolar vascular system of the Tiliaceae to that of the Sterculiaceae.

(ii) FROM WOOD STRUCTURE

Kukachka and Rees (1295) have made a detailed study of the systematic anatomy of the woods of this family. They propose the following 9 taxonomic groups and phylogenetic sequence, the sequence being based on several characters, but chiefly on vessel member length and the relative amount of elongation of the fibres ('fibre-vessel length ratio'). Group I: *Althoffia*, *Belotia*, and *Trichospermum*. Group II: *Apeiba*, *Entelea*, *Erinocarpus*, *Helio-carpus*, *Honckenya*, and *Triumfetta*. Group III: *Colona*, *Goethalsia*, *Luehea*, and *Microcos*. Group IV: *Desplatzia*, *Duboscia*, *Glyphea*, and *Grewiopsis*. Group V: *Lueheopsis* and *Mollia*. Group VI: *Grewia* and *Vinticina*. Group VII: *Chartocalyx*, *Schoutenia*, and *Tilia*. Group VIII: *Brownlowia*, *Diplodiscus*, and *Pentace*. Group IX: *Berrya*, *Carpodiptera*, and *Christiana*.

This arrangement is very similar to that proposed by Burret (315), the chief points of difference in the constitution of the groups being the association in

Group III of *Microcos* and *Leuhea* with *Colona* and *Goethalsia* and the inclusion of *Glyphaea* with *Grewiopsis* and *Desplatzia* in Group IV.

Group I, the Trichospermae of Burret, has the most unspecialized wood characters, with *Althoffia* as the most primitive genus, and Groups VIII and IX, which are substantially Burret's Brownlowieae, the most highly specialized. The high position assigned by Burret to his 3 tribes Triumfetteae, Sparmannieae, and Apeibeae is not held to be justified; it is not clear, however, that the authors have made sufficient allowance for the possible influence of the shrubby habit on the characters, such as ray type, by which specialization of the wood is judged. The group is characterized by an unusual type of pith-like parenchyma.

The 4 African genera in Group IV are regarded as an offshoot of *Microcos*; *Grewiopsis* is regarded as a distinct genus and not a synonym of *Desplatzia*. The conclusion reached by Chattaway (373) that *Microcos* is anatomically distinct from *Grewia* is not only upheld but further evidence is provided. The status of *Vinticensa* is regarded as uncertain.

The anatomy of the wood is held to substantiate Burret's transfer of *Chartocalyx* from the Brownlowieae, but not his reduction of the genus to synonymy with *Schoutenia*.

Groups VII and IX are substantially Burret's Brownlowieae and have many characters in common, particularly vessel-parenchyma pitting and ray type; they stand out as distinct from the other groups.

Record (1845) disagrees on anatomical grounds with the suggestion of Gleason that *Goethalsia* should be transferred to the Flacourtiaceae.

The anatomical evidence supporting the separation of the Elaeocarpaceae is discussed under that family.

ECONOMIC USES

Tilia furnishes two well-known timbers, the European Lime or Linden and the American Basswood. Burma Mahogany or Thitka, *Pentace burmanica* Kurz is used in India for high-class furniture, mathematical instruments, boat-building, &c., and Trincomalee Wood, *Berrya ammonilla* Roxb., and Dhaman, *Grewia tiliaefolia* Vahl., are used in Burma and India respectively for shafts, spokes, and the bent parts in carriage and cart construction. Danta, *Cistanthera papaverifera* A. Chev., is sometimes exported from West Africa. The woods of *Heliocarpus* and *Belotia* are very light and soft.

Valuable fibres are obtained from the phloem of several members of the family, the best known being Jute, which is derived from *Corchorus capsularis* Linn., *C. olitorius* Linn., and other species of *Corchorus*. Less familiar fibres are derived from *Grewia*, *Honckenya*, and *Triumfetta*. Jute fibres are polygonal in transverse section, but with rounded or oval lumina, the latter varying considerably in width throughout the length of the individual elements; the transverse section is stained yellow throughout when treated with iodine solution and sulphuric acid; individual elements several mm. long and 17–23 μ wide.

The fibres of *Triumfetta rhomboidea* Jacq. are, according to Pasqualet (1658), in groups of 15–25 cells; individual elements 90 μ long and 4–7 μ broad; thickness of the wall slightly undulating; cell endings pointed, rounded, or

spoon-shaped; fibres in stems 9–12 months old become violet-coloured when treated with ammoniacal fuchsin.

Decoctions of the leaves of *Grewia polygama* Willd. are stated by Coverlid (489) to be used in Australia in cases of dysentery.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

The above description is actually based on other genera besides those mentioned by name in the text. Those mentioned in the text are: Apeiba, Berrya,* Brownlowia, Columbia, Corchorus,* Desplatia, Diplodiscus, Glyphaea,* Grewia,* Mollia, Nesogordonia, Pentace, Sparmannia, Tilia,* Triumphetta, Vasivaea.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Actinophora, (Althoffia), Apeiba, Belotia, Berrya, Brownlowia, Carpodiptera, Christiana, Cistanthera, Columbia, Desplatia, Diplodiscus, Duboscia, Entelea, Erinocarpus, Glyphaea, Goethalsia, Grewia, Heliocarpus, Luehea, Lueheopsis, Microcos, Mollia, Mortoniodendron, Pentace, Pityranthe, (Schoutenia), Sparmannia, Tilia, Trichospermum, Triumphetta, (Vinticina).

LITERATURE

(i) On General Anatomy

Beauvisage 163, Burret 315, Coverlid 489, Danila 538, Dehay 560, Gehrig 753, Kundu 1302, Mullan 1571, Pasqualet 1658, Richter 1934, Sabnis 1977, Starr 2188, Zebe 2504.

(ii) On Wood Structure

Baehni 62, Bausch 154, Benoist 169, den Berger 179, 182, Besson 186, Bienfait 197, Brown, H. P. 228, 229, Burgerstein 310, Chalk 364, 365, Chattaway 371, 372, 373, Coster 481, Cozzo 494, Edlin 622, Greguss 2522, Hale 870, Horn 1084, Howard 1088, Hyde 1117, Janssonius 1154, Jayawardana 1159, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Kukachka and Rees 1295, Lecomte 1334, Nicoloff 1593, Pearson and Brown 1679, Pereira 1687, Record 1781, 1783, 1808, 1809, 1818, 1843, 1845, 1851, 1871, 1872, 1873–4, 1885, Record and Hess 1886, Record and Mell 1894, Stone 2203, Tang 2231, Williams 2426, 2430, Yamabayashi 2478.

67. ELAEOCARPACEAE

(FIG. 60 on p. 244; FIG. 64 on p. 264; FIG. 65 on p. 270)

SUMMARY

(i) GENERAL

A small tropical and sub-tropical family allied to and at one time included in the Tiliaceae. Although possessing characters in common with the Tiliaceae, the Elaeocarpaceae are distinguished by the lack of **mucilage cavities** and **canals**, although mucilage cells are known to occur. The members of the Elaeocarpaceae which have been examined anatomically do not exhibit triangular stratified **phloem** strands in transverse sections of the stem, nor are the distal ends of the rays triangular. Large cluster **crystals** are common, as in the Tiliaceae and other related families, but Gehrig (753) found solitary crystals to be more frequent than druses in the leaf.

(ii) WOOD

(a) *Excluding Dicraspidia and Muntingia*

Vessels usually rather small, with pronounced radial multiples in some genera, perforations simple, sometimes accompanied by a few vestigial scalariform plates; intervacular pitting large, usually opposite, occasionally alternate; elongated, simple pits to ray cells common; members moderately short to moderately long. **Parenchyma** paratracheal, very sparse; sometimes terminal. **Rays** commonly of 2 sizes, the larger 4–9 cells wide, more than 1 mm. high, and markedly heterogeneous. **Fibres** with small bordered pits, septate in nearly all the genera, moderately short to moderately long. **Intercellular canals** of the vertical traumatic type sometimes present.

(b) *Dicraspidia and Muntingia*

These genera differ from the others mainly in having solitary vessels, small, alternate intervacular pitting and similar pits to ray cells, parenchyma apotracheal and storied, and few uniseriate rays.

LEAF

Usually dorsiventral. Simple unicellular and glandular **hairs** recorded in *Sloanea*. Cells of the **epidermis** frequently mucilaginous. **Stomata**, in species of *Elaeocarpus* and *Sloanea* examined by Gehrig (753), confined to the lower surface. **Hydathodes** stated to be present in *Aristotelia macqui* L'Hérit. Vascular bundles of the **veins**, in species of *Elaeocarpus* and *Sloanea* examined by Gehrig (753), surrounded by 3 or 4 layers of sclerenchyma. **Petiole**, in transverse sections through the distal end, exhibiting a slightly interrupted vascular ring in *Aristotelia macqui* (Fig. 60 E) and *Elaeocarpus serratus* Linn. (Fig. 65 A), the ring being accompanied by 2 strands in *A. macqui* and several accessory strands towards the wings in *Elaeocarpus serratus*. Petiole of *Tricuspidaria dependens* Ruiz. et Pav. as illustrated in Fig. 65 C. **Crystals** mostly solitary in species of *Elaeocarpus* and *Sloanea* examined by Gehrig (753), but clusters also present beside the vascular bundles, e.g. in *Sloanea dentata* Linn.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis. **Cortex** frequently differentiated into an outer collenchymatous and an inner parenchymatous but somewhat spongy zone. **Pericycle** including a somewhat interrupted to almost continuous ring of fibres in certain species of *Aristotelia*, *Elaeocarpus*, and *Tricuspidaria*. The triangular shape of the phloem strands and distal ends of the rays, which are characteristic of the Tiliaceae, have not been observed in species of *Aristotelia*, *Elaeocarpus*, and *Tricuspidaria* available for examination. **Phloem** and **xylem** in the form of closed cylinders traversed by narrow rays. Vessels with mostly simple perforations and occasional scalariform plates. **Pith** usually somewhat heterogeneous.

WOOD

(a) *Excluding Dicraspidia and Muntingia* (Fig. 64 A-F)

Vessels usually very to moderately small ($25\text{--}100\ \mu$ mean tangential diameter), medium-sized ($100\text{--}200\ \mu$) in some species of *Elaeocarpus*; commonly with radial multiples of 4 or more in *Aristotelia*, *Crinodendron* (Fig. 64 E),

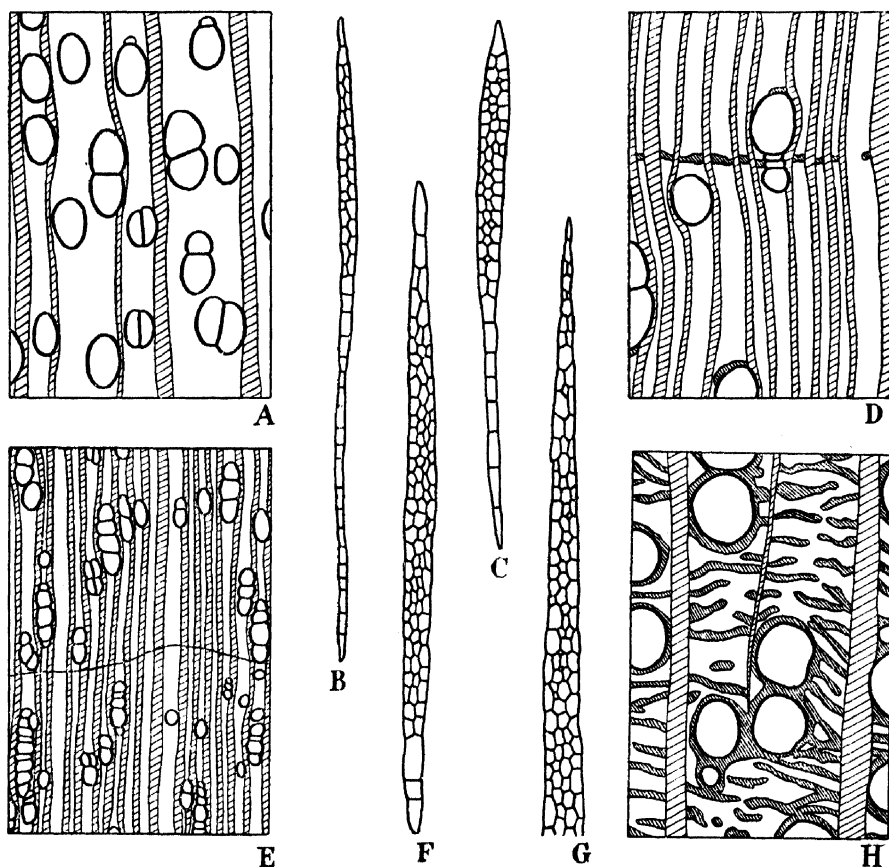


FIG. 64. ELAEOCARPACEAE

A, *Sloanea australis* F. v. M. B, *Vallea stipularis* Linn. C, *Elaeocarpus grandis* F. v. M. D, *E. floribundus* Bl. E, *Crinodendron tucumanum* Lillo. F, *Sloanea australis* F. v. M. G, *Dicraspidia donnell-smithii* Standl. H, *D. donnell-smithii* Standl.

many species of *Elaeocarpus*, *Tricuspidaria*, and *Vallea*. Fewest, about 5–20 per sq. mm., in *Elaeocarpus* and *Sloanea* p.p., most numerous, 40 or more per sq. mm., in *Aristotelia*, *Crinodendron*, and *Vallea*; spiral thickening present in some species of *Elaeocarpus*. Perforation plates exclusively simple in most genera and oblique, but some vestigial scalariform plates occur in *Aristotelia* and *Vallea* (1295). Intervascular pitting large; typically opposite, but alternate or transitional to alternate in *Crinodendron* and *Vallea* p.p. (1295); pits to ray and wood parenchyma frequently simple and often elongated horizontally (less commonly so in *Elaeocarpus*) or unilaterally compound.

Solid deposits and tyloses present in some species. Mean member length 0.4–1.0 mm. **Parenchyma** paratracheal and in narrow terminal bands (Fig. 64 D); the paratracheal parenchyma usually limited to a few cells round the vessels and sometimes extremely sparse or absent, e.g. in *Aristotelia* and *Vallea*; in narrow sheaths round the vessels, confluent, and diffuse in *Echinocarpus* (1295). **Rays** up to 2–3 cells wide in *Aristotelia*, *Crinodendron*, *Tricuspidaria*, and *Vallea*; 4–10 cells wide in *Echinocarpus*, *Elaeocarpus*, and *Sloanea*; of 2 distinct sizes in *Aristotelia*, *Elaeocarpus*, *Sloanea*, and *Tricuspidaria*; the larger rays more than 1 mm. high, except in *Tricuspidaria* and *Vallea*; uniseriate numerous and typically composed entirely of upright cells, but with some procumbent cells in *Vallea*; about 10–20 rays per mm.; heterogeneous (Kribs's Types I and II A), with wide margins of 10 or more square to upright cells; sheath cells often present. Sometimes containing dark deposits; crystals in chambered upright cells prominent in most species of *Elaeocarpus* and occasionally present in *Crinodendron*; silica present in some species of *Elaeocarpus* (794). **Fibres** with small bordered pits that are more numerous in the radial than in the tangential walls, the borders sometimes very inconspicuous. Septate in *Aristotelia*, *Crinodendron*, *Elaeocarpus*, *Sloanea*, *Tricuspidaria*, and *Vallea*, the septa sometimes limited to the fibres adjoining the vessels. Walls never very thick and usually thin. Janssonius (1154) refers to the presence of occasional solitary crystals in the septate fibres of *Sloanea sign* K. Schum. Mean length 0.7–1.9 mm. **Inter-cellular canals** of the vertical traumatic type reported (1801) in *Elaeocarpus* and *Sloanea*.

(b) *Dicraspidia* and *Muntingia* (Fig. 64 G–H)

These 2 genera resemble each other very closely, but differ from the rest of the family, particularly in the following features.

Vessels mostly solitary; semi-ring-porous in *Muntingia* (1851); inter-vascular pitting small and alternate and pits to ray cells similar; mean member length in *Muntingia* 0.3 mm. (100). **Parenchyma** as (a) uniseriate sheaths round the vessels, and (b) in numerous short uniseriate bands and scattered cells (diffuse) (Fig. 64 H); storied. **Rays** homogeneous in *Muntingia* (1886), composed almost entirely of square and upright cells in *Dicraspidia*. **Fibres** sometimes septate in *Dicraspidia* (376); with simple pits; storied.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The anatomical structure of the members of this family is sufficiently distinct from that of the Tiliaceae to justify treating the Elaeocarpaceae separately.

(ii) FROM WOOD STRUCTURE

Dicraspidia and *Muntingia* differ considerably from the other genera in their wood anatomy. Except for these 2 genera, which have many points in common with the Tiliaceae, and possibly *Echinocarpus*, the wood anatomy supports the establishment of the Elaeocarpaceae as a separate family.

Kukachka and Rees (1295) note that 'practically all the characters of the

Elaeocarpaceae point to a primitive type of structure' and regard the family as distinctly less highly specialized than the Tiliaceae, with *Echinocarpus* as a possible link. These authors, however, do not favour the removal of this genus from the Elaeocarpaceae. Their arrangement of the genera within the family is essentially the same as that of Engler and Prantl, with the tribe Elaeocarpeae in the most primitive position, except that *Sloanea* is placed before *Elaeocarpus* and that *Echinocarpus* is regarded as a genus and not a section under *Sloanea*.

Bausch (154) has suggested that *Eucryphia* may have affinities with this family, but, in the author's opinion, the wood anatomy lends little support to such a view.

ECONOMIC PRODUCTS

The fruits of the Macqui (*Aristotelia macqui* L'Hérit.) are eaten in Chile. None of the timbers are of more than local importance, but some species of *Elaeocarpus* and *Sloanea* are used in Australia for veneers, core-stocks, and cabinet-work.

GENERA DESCRIBED

(i) GENERAL ANATOMY

Aristotelia,* *Elaeocarpus*,* *Muntingia*, *Tricuspidaria*.*

* Represented in the Kew slide collection.

(ii) WOOD STRUCTURE

A. (*Aristotelia*), *Crinodendron*, (*Echinocarpus*), *Elaeocarpus*, *Sloanea*, *Tricuspidaria*, *Vallea*.

B. *Dicraspidia*, (*Muntingia*).

LITERATURE

(i) *On General Anatomy*

Gehrig 753.

(ii) *On Wood Structure*

Bailey and Tupper 100, Bausch 154, Beekman 167, den Berger 179, 182, Brown, F. B. H. 280, Cozzo 494, Dadswell 525, Desch 574, Descole 576, Garratt 744, Gonggrijp 794, Howard 1088, Janssonius 1154, Kanehira 1206, 1209, Kribs 1283, Kukachka and Rees 1295, Pearson and Brown 1679, Record 1801, 1809, 1843, 1851, Record and Hess 1866, Record and Mell 1894, Tang 2231, Williams 2430.

68. SCYTOPETALACEAE

(FIG. 66 on p. 276)

SUMMARY

A small family of trees from west tropical Africa. The wood exhibits the following characters. **Vessels** with simple perforations and a few scalariform perforation plates, intervacular pitting alternate, pits to parenchyma elongated and almost simple, members of medium length. **Parenchyma** apotracheal, in numerous uniseriate bands. **Rays** up to 6 cells wide, with rather few uniseriates, heterogeneous. **Fibres** with simple pits and of medium length.

LEAF

Usually dorsiventral, but palisade tissue not always distinct. **Hairs**, where present, simple and unicellular. Cells of the **epidermis** sometimes elongated and divided by tangential walls in *Oubanguia* and *Scytopetalum*; inner walls convexly arched and some of the cells filled with red contents in *Brazzeia*. **Stomata** present on both surfaces or confined to the lower side; cruciferous. All subsidiary cells filled with violet contents in *Oubanguia* and *Rhaptopetalum*, but similar contents confined to the smallest subsidiary cell in *Brazzeia*, and absent altogether from *Scytopetalum*. **Mesophyll** containing idioblasts connected with the sclerenchyma of the veins and spreading out beneath the epidermis, in all 4 genera, but not in all of the species of each genus. An arc-shaped vascular strand passes out to the leaf from the axis, but the **petiole** is stated, in transverse sections, to exhibit a large median and 2 smaller lateral strands.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis or outer part of the cortex in *Oubanguia*, and from the epidermis itself in *Brazzeia*, *Rhaptopetalum*, and *Scytopetalum*; cork cells with U-shaped thickenings in *Rhaptopetalum*. **Pericycle** containing isolated bundles of fibres. **Phloem** stratified into lignified and unlignified portions. **Xylem** traversed by rays 1-3 cells wide and including abundant parenchyma. Vessels of *Scytopetalum klaineianum* Pierre exhibiting a wide range of diameter and provided with scalariform and reticulate lateral thickening as well as steep scalariform perforation plates. Two **cortical vascular bundles** commonly present. '**Cristarque cells**' (i.e. cells with U-shaped thickenings containing crystals, cf. Ochnaceae) present in all parts of the primary cortex of *Oubanguia* and *Scytopetalum*, but not recorded for *Rhaptopetalum*.

WOOD (Fig. 66 J-K)

Vessels medium-sized (100-200 μ mean tangential diameter); solitary and in multiples of 2 or 3 cells; about 3 per sq. mm. Perforations mostly simple, but some scalariform plates, with up to 12 bars, usually present. Intervascular pitting alternate and rather small; pits to ray and wood parenchyma cells often large and simple and arranged in scalariform groups with the long axes of the pits horizontal, vertical, or oblique. Mean member length about 0.5 mm. **Parenchyma** apotracheal, in very numerous uniseriate bands and scattered among the fibres. Strands usually of 8 cells. **Rays** up to 6 cells wide; rays less than 1 mm. high; uniseriates few and composed of both procumbent and upright cells; about 9 rays per mm.; heterogeneous (Kribs's Type II B), with 1 or 2 marginal rows of square to slightly upright cells. **Fibres** with simple pits, equally numerous on both radial and tangential walls. Walls very thick. Mean length 1.1 mm.

TAXONOMIC NOTES

This small family is included in the Malvales in the Engler system and in the Tiliales by Hutchinson (1113). *Rhaptopetalum* was treated in the Bentham

and Hooker system as an anomalous genus under Olacineae. Of the rather limited facts recorded about the anatomy of the family, the occurrence of phloem stratified into lignified and unlignified portions is somewhat suggestive of affinities with the Tiliaceae; the wood anatomy is also not inconsistent with such a view, but is of a less highly specialized type. On the other hand, 'cristarque cells' have not been recorded in the Tiliaceae although they are a characteristic feature in some of the Scytopetalaceae. It is interesting to note that these rather uncommon elements also occur in the Ochnaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Brazzeia, *Oubanguia*, *Rhaptopetalum*, *Scytopetalum*.

(ii) FOR WOOD STRUCTURE

Scytopetalum.

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113.

(ii) *On Wood Structure*

Cooper and Record 461, Record 1851.

69. LINACEAE

(FIG. 65 on p. 270; FIG. 66 on p. 276)

SUMMARY

(i) GENERAL

Most of the Linaceae are shrubs and small trees from tropical regions, although a few herbaceous genera such as *Linum* and *Radiola* flourish in cooler climates. The family also includes woody climbers which are supported by **tendrils** resembling coiled watch springs which arise from the secondary branches. The anatomical structure of the leaves and young shoots of the woody species is known only very incompletely. The most familiar feature in *Linum* is the well-defined masses of fibres in the **pericycle** of the stem, where they are sometimes sufficiently close together to form an almost continuous ring. The cells of the **epidermis** are often mucilaginous in *Hugonia* and *Linum*. **Stomata** are usually rubiaceous. **Crystals** mostly solitary except in *Reinwardtia* sp., where clustered crystals occur in the cortex of the stem. The **xylem** and **phloem** are in the form of continuous cylinders in *Linum* except in very young stems, where the bundles are individually distinct but not very widely separated.

(ii) Wood

Vessels exclusively solitary except in *Hugonia*, perforation plates scalariform or simple, pits to ray cells small and bordered or large and simple; members moderately to very long. **Parenchyma** very varied in different genera, mostly aliform or confluent and sometimes abaxial; in broad, blunt-

ended bands dissociated from the vessels in some genera. **Rays** up to 2–5 cells wide, markedly heterogeneous. **Fibres** with numerous distinctly bordered pits, grading to tracheids adjoining the vessels, of medium length to moderately long.

LEAF

Generally dorsiventral, but mesophyll not clearly differentiated into palisade and spongy regions in *Linum usitatissimum* Linn. **Hairs** usually consisting of narrow, unicellular (more rarely multicellular) trichomes of varying length. Glandular shaggy hairs recorded on the leaf margin of *Linum viscosum* Linn.; tufted hairs apparently confined to *Ctenolophon*. Cells of the **epidermis** with straight or sinuous anticlinal walls; sometimes mucilaginous in certain species of *Hugonia*, *Linum*, and *Roucheria*. **Stomata** usually confined to the lower surface, but present on both sides in *Linum usitatissimum* and in at least some of the other species of *Linum*; rubiaceous in *Linum*, *Radiola*, and *Reinwardtia*. A single layer of **hypoderm** recorded in *Ixonanthes* sp. **Mesophyll** including idioblasts in *Hugonia* and *Ochthocosmus* sp. Spiral tracheae, similar to those of *Nepenthes*, occur in the mesophyll of *Ochthocosmus roraimae* Benth. Vascular bundles of the **veins** accompanied by well-developed sclerenchyma. Three bundles pass out from the axis to the base of the leaf in *Ctenolophon*, *Hugonia*, *Ixonanthes*, *Roucheria*. **Petiole** of *Reinwardtia trigyna* Planch. (Fig. 65 B) with a shallow, crescentic vascular strand in transverse sections through the distal end.

AXIS

STEM (Fig. 65 H, J, and L)

Cortex not exhibiting any noteworthy features in *Linum*. **Pericycle** characterized by specially large, conspicuous fibre strands in *Linum* (Fig. 65 J and L), the best known being the flax fibre of commerce derived from *L. usitatissimum* Linn. (see 'Economic Uses' on p. 272). Pericyclic fibres absent, e.g. from *Reinwardtia trigyna* Planch. (Fig. 65 H). **Xylem** and **phloem** constituting closed cylinders traversed by narrow medullary rays in mature stems of *Linum*, but bundles individually distinct near the stem apex in the same genus. Vessels of *Linum* mostly in radial rows, but in some species tending to be solitary, or, more rarely, in tangential pairs; perforations simple (see also 'Wood'). **Pith** becoming hollow in *Linum*.

WOOD (Fig. 66 A–D and G)

Vessels medium-sized (100–200 μ mean tangential diameter), largest in *Hugonia*; exclusively solitary, except in *Hugonia* and *Lepidobotrys*, in which a few radial multiples of 2 or 3 cells occur; 3–30 per sq. mm., most numerous in *Ctenolophon*. Spiral thickening reported by Solereder in *Indorouchera griffithiana* (Planch.) Hallier. Perforation plates scalariform in *Ctenolophon* and *Indorouchera* (938), usually with less than 25, rather thick bars, but the bars more numerous and often anastomosing in *C. englerianus* Mildbr.; exclusively or predominantly simple in the other genera. Intervascular pitting very rare except in *Hugonia*, in which the pits are moderately large and alternate, with round borders and horizontal, frequently coalescing apertures, and *Lepidobotrys*, with minute alternate pitting. Pits to ray cells

sionally present in *Ochthocosmus africanus* Hook. f.; solid deposits rare. Mean member length 0.7 (*Ixonanthes*) to 1.25 mm. (*Ctenolophon*). **Parenchyma** often difficult to classify as either paratracheal or apotracheal; in *Ctenolophon* and *Roucheria calophylla* Planch. (Heimsch 938) forming uniseriate rows along the abaxial sides of the vessels and extending tangentially as narrow wings that spring usually from the tops of the vessels but sometimes from the sides; in *Ixonanthes* and *Ochthocosmus* and, according to Heimsch (938), in *Phyllocosmus* in bands 2–3 cells wide that start and end blindly, as in confluent parenchyma, but independently of the vessels; aliform in *Hebepetalum*; aliform and confluent in *Hugonia*; with scanty paratracheal parenchyma, according to Heimsch, in *Linum*, *Reinwardtia*, and *Roucheria*, vasicentric in the latter and in *Tirpitzia*; abundant, as scattered cells, in *Lepidobotrys*; Heimsch describes the parenchyma in *Indorouchera* as 'abundant diffuse-in-aggregate with a strong tendency to form narrow apotracheal bands'. Cells usually filled with a dark gum-like substance; crystals in chambered cells present in some species, particularly of *Ctenolophon*, *Lepidobotrys*, and *Ochthocosmus* and very abundant in *Hugonia*. Heimsch has observed sclerotic parenchyma cells in *Hebepetalum*. Strands usually of 8 cells, often up to 16 cells in *Ctenolophon*. **Rays** multiseriate, up to 2 or 3 cells wide in *Ctenolophon*, *Hebepetalum*, *Ixonanthes* (4 cells wide in *I. reticulate* Jack.), and *Ochthocosmus* and up to 5 cells wide in *Hugonia*; rays almost exclusively uniseriate in *Lepidobotrys* and, according to Heimsch, in some species of *Ixonanthes* and *Ochthocosmus*; commonly about 1.5 mm. high in *Ctenolophon* and *Hugonia*, less than 1 mm. in the other genera; uniseriate rays numerous, composed entirely of upright cells in *Ctenolophon* and *Hebepetalum*, mostly of procumbent cells in the other genera; 9–12 rays per mm.; heterogeneous (Kribs's Types I–II B and occasionally III), with uniseriate margins of 4 or more rows of square or upright cells; often with more than 10 rows in *Ctenolophon* and *Hugonia*; almost homogeneous in *Lepidobotrys*; the multiseriate part of the ray sometimes only a few cells high and not much wider than the uniseriate margins. Cells with conspicuous gum-like contents; with chambered crystals in *Ctenolophon englerianus* and *Hebepetalum*. **Fibres** with numerous bordered pits on all walls except in *Ixonanthes* and *Lepidobotrys*, in which the pits are more numerous on the tangential walls and with only minute borders in the latter. Walls moderately thick to thick. Cells near the vessels often with thinner walls, wider lumina, and more numerous pits, with all gradations from the long fibre-tracheids of the ground tissue to short **vasicentric tracheids**. Mean length 1.0 (*Ixonanthes*) to 2.0 mm. (*Ctenolophon*).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The anatomical structure differs considerably from that of the Erythroxylaceae which was included in this family by Bentham and Hooker. The Erythroxylaceae have, therefore, been described separately. It has recently been suggested that *Ctenolophon* may have affinities with the Humiriaceae (see 'Humiriaceae').

(ii) FROM WOOD STRUCTURE

The marked differences between genera strongly suggest that this family is

not a sound natural group. *Ctenolophon*, which has a much more primitive structure than the other genera, except possibly *Indorouchera*, bears a close resemblance to the Humiriaceae.

Heimsch (938) appears to regard the differences between the other genera of the Linaceae and those of the Humiriaceae as compatible with the obviously greater degree of specialization in the former. Indeed, he states that 'no evidence from xylem structure militates against a union of these families as is done by Hallier and Winkler', but he does not approve of Hallier's proposal to transfer *Ctenolophon* to the Celastraceae.

The rather unusual type of parenchyma band found in *Ixonanthes*, *Ochthocosmus*, and *Phyllocosmus*, together with the tendency to an oblique vessel pattern and vasicentric tracheids, is suggestive of affinity with the Calophylloideae group of the Guttiferae and *Vismia* of the Hypericaceae.

Lepidobotrys, as judged by a single twig of *L. staudtii* Engl., is exceptional in many respects, but almost all its features, taken singly, can be matched in some other genus, suggesting that, while it has affinities with the Linaceae, it stands somewhat apart from the other genera.

ECONOMIC USES

The most important economic plant in this family is flax, the commercial types of which are derived from varieties of *Linum usitatissimum* Linn. Linseed oil is expressed from the seeds of the same species. The residue left after expressing the oil is used to manufacture cattle cake. Best-quality flax is obtained from specially selected varieties grown close together so as to induce long, slender, unbranched stems. According to Djakonov (593) the quantity of fibre present in the stem appears to depend on the moisture content of the soil. Individual fibre elements are mostly 12–25 μ in diameter (greater in fibres from the base of the stem and root) and from about 20 to 40 or more mm. long, the longest fibres being in the upper part of the stem. In rare instances the fibres may be as much as 120 mm. long while the diameter has been recorded as ranging from 9.6 to 201.6 μ . The secondary walls are divided into 2–5 major layers, composed mainly of cellulose but becoming lignified to a greater or less extent during development, the amount of lignin varying in different parts of the plant. The middle lamella is at first composed of pectic substances, but later tends to become lignified. Fibres sharply polygonal in transverse section, the lumen usually very small, but broader in fibres from the base of the stem or from the root. Fibres from the root very similar to those of Hemp (*Cannabis sativa*), but stated by Korn (1268) to be distinguishable by differential staining with basic dyes, by treatment with ammoniacal copper oxide, or according to Sonntag (2166) by an intensive study of differences in the striation of the cell wall. Cell endings usually pointed, but sometimes rounded, this difference depending on the position within the plant from which they have been derived. For further particulars of fibre structure see Wiesner (2423), Hayward (927), Kremer (1280), and, for the comparative stem structure of closely related species and varieties of *Linum*, the articles by Melkinov (1488, 1489) and Nestler (1587). The developmental anatomy of the flax plant has been summarized by Hector (929), Hayward (927), and Esau (656, 657). For further microscopical differences between the fibre of flax and hemp see 'Cannabinaceae—Economic Uses'.

GENERA DESCRIBED

(i) GENERAL ANATOMY

Ctenolophon, Hugonia, Ixonanthes, Linum,* Ochthocosmus, Radiola, Reinwardtia,* Roucheria.

* Represented in the Kew slide collection.

(ii) WOOD STRUCTURE

Ctenolophon, Hebeptalum, Hugonia, (Indorouchera), Ixonanthes, Lepidobotrys (twig only), (Linum), Ochthocosmus, (Phyllocosmus), (Reinwardtia), (Roucheria), (Tirpitzia).

LITERATURE

(i) *On General Anatomy*

Crooks 508, Djakonov 593, Esau 656, 657, Hayward 927, Hector 929, Korn 1268, Kremer 1280, Melnikov 1488, 1489, Nestler 1587, Sonntag 2166, Tever 2244, Tobler 2266, Wiesner 2423, Winkler 2441.

(ii) *On Wood Structure*

Bausch 154, den Berger 182, Burgerstein 312, Heimsch 938, Kanehira 1206, Lecomte 1334, Record 1843, 1851, Record and Hess 1886.

70. ERYTHROXYLACEAE

(FIG. 65 on p. 270; FIG. 66 on p. 276)

SUMMARY

(i) GENERAL

A family of trees and shrubs wholly confined to the tropics. The more noteworthy anatomical features are the usually abundant, prismatic, solitary **crystals** present in the parenchymatous tissues, especially the epidermal cells; the presence of sclerenchymatous idioblasts in the **mesophyll** of the leaf; the superficial origin of the **cork** in the stem, and the existence of **cortical bundles** in the young stem. The **xylem** and **phloem** in young stems constitute continuous cylinders traversed by narrow rays.

(ii) WOOD

Vessels occasionally tending to form long radial multiples, perforations simple, intervacular pitting alternate and very small, pits to parenchyma elongated and almost simple, members of medium length. **Parenchyma** predominantly paratracheal with a little diffuse, the paratracheal as vasicentric, aliform or confluent. **Rays** 2-5 cells wide, heterogeneous. **Fibres** with distinctly bordered to simple pits, of medium length.

LEAF

Generally dorsiventral; approximately centric in a few species of *Erythroxylum*. Cells of the **epidermis** mucilaginous in certain species of *Aneulophus* and *Erythroxylum*. Lower epidermis frequently papillose in *Erythroxylum* spp. and in *Nectaropetalum kaessneri* Engl. but not in *N. capense* O. Stapf. **Stomata** confined to the lower surface; rubiaceous in the species of *Erythroxylum* used as the source of cocaine (see 'Economic Uses'), and in *Nectaropetalum*. **Mesophyll** commonly including sclerenchymatous idioblasts in *Erythroxylum* spp. Vascular bundles of the **veins** in *Nectaropetalum capense*

embedded in the mesophyll, but accompanied by sclerenchyma. Three bundles enter the base of the **petiole**, the two lateral ones giving off branches to the stipules, but then uniting with the main arc-shaped vascular strand in the distal end. Minor differences occur in the arrangement of the vascular system of the petiole of *Aneulophus* and *Erythroxylum* respectively. Scattered solitary **crystals** occur in the palisade tissue and in the parenchymatous tissues of the petiole of *Erythroxylum coca* Lam.

The structure of the epidermis, the form of the palisade cells, the structure of the midrib, the occurrence and distribution of papillae and sclerenchyma provide characters which have enabled a table for the identification of different species of *Erythroxylum* to be drawn up (Ballard 116).

AXIS

YOUNG STEM (Fig. 65 K)

Cork arising in the epidermis of *Aneulophus* and in the sub-epidermis of *Erythroxylum*. **Pericycle** containing isolated groups of fibres in *Erythroxylum* and *Nectaropetalum*, but a composite, continuous ring of sclerenchyma present in *Aneulophus*. **Phloem** constituting a continuous cylinder, containing scattered groups of fibres or stone cells in different species of *Erythroxylum*, but provided with a practically continuous ring of sclerenchyma in *Aneulophus*. Secondary phloem stratified into lignified and unlignified portions in *Nectaropetalum*. **Xylem** also in the form of a closed cylinder traversed by narrow rays. Vessels rather unevenly distributed, tending to be in radial rows of about 2-6; perforations simple. See also 'Wood'. **Cortical bundles** (Fig. 65 K) usually present in stems which are sufficiently young.

The following statement by Boodle [see Stapf and Boodle (2187)] concerning the cortical bundles of *Nectaropetalum kaessneri* Engl. is quoted verbatim.

'In *Nectaropetalum* two vascular bundles separate from the stele in the upper part of the internode and pass upwards, as cortical bundles, through the node and the next internode. They reach the second node, where apparently each of them forks into two, one branch going to the leaf trace and one to the stipule. It follows that there are two cortical bundles in the lower part of an internode, and four in the upper part. Thus the behaviour of the cortical bundles is similar to that of the cortical bundles in *Erythroxylum*, except that in that genus, according to Van Tieghem (2318) the cortical bundles originate in the lower, instead of the upper, portion of the internode, and stop at the next node, instead of the next but one. In *Erythroxylum emarginatum* Schum. et Th., the two bundles originate practically at the node, but one or both may separate from the stele just before or just after the two cortical bundles from the node below pass out of the stem. Hence, as regards the cortical bundles, this species forms a connecting link between *Nectaropetalum kaessneri* and the species of *Erythroxylum* investigated by Van Tieghem.'

Secretory cells with gum-like contents numerous in the cortex of *Erythroxylum coca* Lam. Solitary, octahedral **crystals** occur in scattered cells in the cortex, phloem, and pith of *Erythroxylum coca*, being most numerous in the cortex.

WOOD (Fig. 66 E-F, H-I, L)

Vessels small (50-100 μ mean tangential diameter) to medium-sized (100-200 μ); solitary and in multiples, some of the multiples of 4 or more

cells in most species; with a tendency to form oblique rows in *E. mannii* Oliv.; usually 12–40 per sq. mm. Perforations typically simple, and Heimsch (938) states that they are so without exception; Williams (2430), however, refers to a few scalariform plates. Intervascular pitting alternate and very small; pits to ray and wood parenchyma often elongated and almost simple, and tending to form scalariform groups with the long axes of the pits horizontal, vertical, or oblique. Tyloses sometimes present. Mean member length 0.4–0.8 mm. **Parenchyma** variable and often difficult to classify, suggesting an intermediate type between apotracheal and paratracheal. Predominantly paratracheal in most of the material examined, e.g. in *E. cuneatum* Kurz., *E. mannii* (Fig. 66 E), and *E. monogynum* Roxb. as complete to partial sheaths, sometimes limited to the abaxial sides of the vessels, aliform or confluent, and usually with some scattered cells in addition, the latter abundant in *E. cuneatum*. Chambered crystals usually abundant. Strands mostly of 6–8 cells. **Rays** up to 2–5 cells wide; typically less than 1 mm. high; uniseriate moderately to very numerous, composed of mixed upright and procumbent cells; 6–12 rays per mm.; heterogeneous (Kribs's Type II B), with up to 6–8 marginal rows of square to upright cells. **Fibres.** Heimsch (938) states that the fibrous elements consist of tracheids or fibre-tracheids; the borders, however, are sometimes very small, e.g. in *E. burmanicum* Griff. and *E. mannii*. Walls thick. Mean length 1.1–2.8 mm.

BARK

The smooth periderm becomes perforated by the development of wart-like lenticels, usually scattered, but, in some species, in longitudinal rows. Cork exceptionally well developed in certain species of *Erythroxylum*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The genera in this family were, in the Bentham and Hooker system, included in the Linaceae, but they are now generally treated as a separate but related family.

The existence of cortical bundles in *Nectaropetalum capense* O. Stapf was believed by Boodle to lend support to Stapf's (Stapf and Boodle 2187) opinion that this species, which had previously been known as *Peglara capensis* Bolus and tentatively assigned to the Rhizophoraceae, is, in reality, congeneric with *Nectaropetalum* belonging to the Erythroxylaceae.

(ii) FROM WOOD STRUCTURE

Heimsch (938) considers that, on the basis of the wood anatomy, the closest affinities of the family lie with the Linaceae rather than with any other family, but that these two families are distinct.

ECONOMIC USES

Cocaine is derived from the leaves of *Erythroxylum* spp. The most important commercial types are Huanuco or Bolivian Coca (*E. coca* Lam.) and Truxillo or Peruvian Coca (*E. truxillense* Rusby). The shortly petiolate, oval to lanceolate or occasionally ovate, somewhat leathery, glabrous, bitter leaves of *E. coca* exhibit the following diagnostic microscopical features. The upper

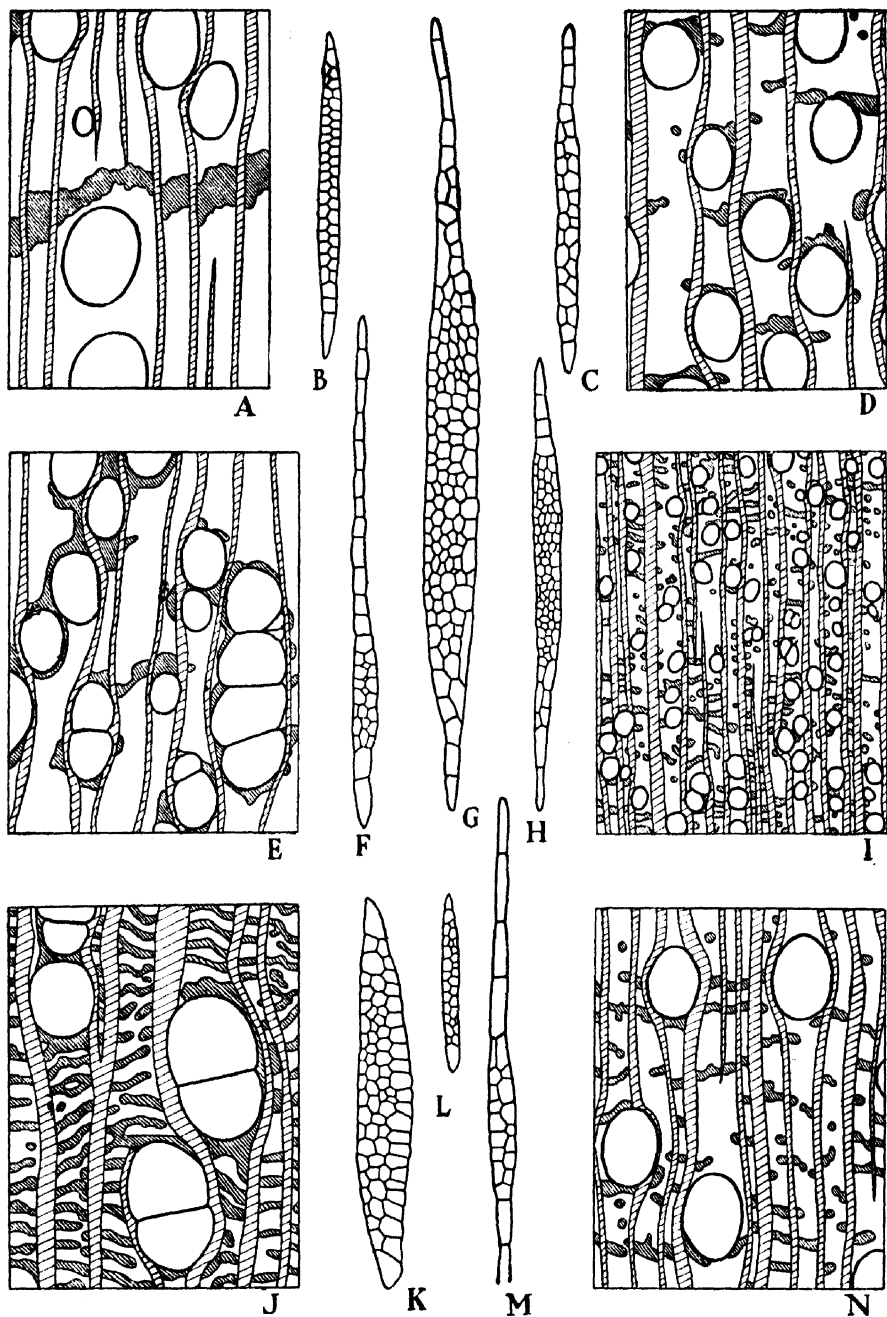


FIG. 66. LINACEAE, A-D and G; ERYTHROXYLACEAE, E-F, H-I, and L;
SCYTOPETALACEAE, J-K; HUMIRIACEAE, M-N

A, *Ixonanthes reticulata* Jack. B, *Ochthocosmos africanus* Hook. f. C, *Ixonanthes reticulata* Jack. D, *Ctenolophon grandifolius* Oliv. E, *Erythroxylum mannii* Oliv. F, *E. burmanicum* Griff. G, *Ctenolophon grandifolius* Oliv. H, *Erythroxylum cuneatum* Kurz. I, *E. burmanicum* Griff. J, *Scytopetalum tieghemii* Hutch. et Dalz. K, *S. tieghemii* Hutch. et Dalz. L, *Erythroxylum mannii* Oliv. M, *Saccolottis gabonensis* Urb. N, *S. gabonensis* Urb.

epidermis composed of cells which appear quadratic in transverse sections; the lower epidermis consisting of papillose cells; the rubiaceous stomata confined to the lower surface; the single layer of palisade cells, some of which are divided and contain solitary crystals; the small vascular bundles embedded in the spongy parenchyma where they are accompanied by a few fibres.

According to Levin (1366), the vein islet number of *Erythroxylum coca* Lam. is said to vary from 8 to 12, as compared with 15 to 26 in *E. truxillense* Rusby, thus serving to distinguish these two important commercial species.

The timber of *Erythroxylum* is hard, strong, and durable, is used locally in tropical America and West Africa, and has been exported to a limited extent.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aneulophus, *Erythroxylum*, * Nectaropetalum.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Erythroxylum.

LITERATURE

(i) On General Anatomy

Ballard 116, Levin 1366, Schulz 2050, 2054, Stapf and Boodle 2187, van Tieghem 2318.

(ii) On Wood Structure

Besson 186, Desch 574, Heimsch 938, Howard 1088, Link 1377, Metcalfe 1497, Normand 1614, Record 1843, 1851, Record and Hess 1886, Record and Mell 1894, Williams 2430.

✓ 71. HUMIRIACEAE

(FIG. 66 on p. 276)

SUMMARY

(i) GENERAL

Trees or shrubs which occur in tropical America and Africa. The wood exhibits the following characters. **Vessels** solitary, perforation plates exclusively scalariform; members extremely long. **Parenchyma** usually predominantly diffuse with a little vasicentric, but ranging from this to confluent, with or without a little diffuse, the paratracheal parenchyma often abaxial. **Rays** 2 or occasionally 3 cells wide, with conspicuous marginal rows of upright or square cells and filled with gum-like substance. **Fibres** with numerous bordered pits, very long.

LEAF

Leathery and dorsiventral. **Hairs** rare, but simple unicellular or uniseriate trichomes recorded in *Vantanea* sp., and short, conical, unicellular ones in certain species of *Saccoglottis*. External **glands**, with a secretory epidermis of palisade-like cells, occur at the leaf margins of *Humiria*, and appear like dots. Cells of the **epidermis** larger on the upper than on the lower surface in *Humiria* and *Vantanea*, but of equal size on both surfaces in *Saccoglottis*.

Stomata ranunculaceous in *Humiria* and *Saccoglottis*; rubiaceous, accompanied by subsidiary cells parallel to the pore, but divided by a wall perpendicular to the latter in *Vantanea* sp. **Mesophyll**. Palisade cells much more elongated in *Humiria* than in *Saccoglottis* and *Vantanea*. Sclerenchymatous idioblasts extend from one epidermis to the other in certain species of *Saccoglottis*. Clustered **crystals** present in the mesophyll in *Humiria* sp. and solitary ones in *Saccoglottis* sp.

AXIS

YOUNG STEM

Cork sub-epidermal in *Humiria* and *Saccoglottis*; cells thin-walled and somewhat compressed in a radial direction. Primary **cortex** containing stone cells in certain species of *Humiria* and *Saccoglottis*. **Pericycle** including a composite and continuous ring of sclerenchyma in certain species of *Aubrya*, *Humiria*, and *Vantanea*. Secondary **phloem** containing fibres. Distal ends of the medullary rays, where traversing the phloem, sclerosed in certain species of *Humiria* and *Saccoglottis*. **Xylem** in the form of a continuous cylinder traversed by narrow rays; vessels with scalariform perforation plates. Solitary **crystals** present in cells adjoining the sclerenchyma of the phloem, and clustered ones in the soft tissue in the same region.

WOOD (Fig. 66 M-N)

Vessels medium-sized (mean tangential diameter 100–200 μ); exclusively solitary or nearly so; 6–10 per sq. mm. Perforation plates scalariform with 15–25 bars, which are usually rather thick. Intervascular pitting rare; when present, opposite to alternate and moderately large; pits to ray cells and parenchyma similar to the intervascular pitting, round to oval with horizontal apertures in *Humiria* and *Saccoglottis*; in *Vantanea* these pits are simple or with transitional borders (2158) and often oblong or scalariform (938). Mean member length 1.8–2.0 mm. **Parenchyma** typically both apotracheal and paratracheal; most commonly with scattered cells predominating and tending to form short uniseriate lines, e.g. in *Saccoglottis gabonensis* Urb. (Fig. 66 N) and *Humiria*; the paratracheal parenchyma tending to be abaxial, and with distinct wings in *Saccoglottis obovata* Engl. and *Vantanea* p.p. Chambered crystal cells present in woods with well-developed paratracheal parenchyma. **Rays** typically up to 2 or 3 cells wide; occasionally up to 4 cells in some species (938); almost uniseriate in *Saccoglottis obovata*; rays often slightly more than 1 mm. high; uniseriates numerous, and composed of procumbent and square to upright cells; about 12 rays per mm.; heterogeneous (Kribs's Type II A?), with more than 4 marginal rows of square to upright cells (often more than 10 rows in *Saccoglottis*), which are not much narrower than the biseriate parts. Cells often filled with dark contents. **Fibres** with numerous, distinctly bordered pits on both radial and tangential walls; walls thick. Mean length about 2.2 mm.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The idioblasts in the mesophyll of *Saccoglottis* recall those which occur in members of the Theaceae.

(ii) FROM WOOD STRUCTURE

Heimsch (938) considers that this family forms a homogeneous group, distinct from the Linaceae, but more nearly related to it than to any other family; the greatest resemblance is to *Ctenolophon*, which he believes has closer affinities with the Humiriaceae than with the Linaceae. The woods of the Humiriaceae are more unspecialized than those of the Linaceae, except that of *Ctenolophon*.

ECONOMIC USES

The timbers of this family are dense; they are of little importance, though some species of *Humiria* are used in tropical America for heavy construction, wheels, &c.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aubrya, Humiria, Saccoglottis, Vantanea.

(ii) FOR WOOD STRUCTURE

Humiria, Saccoglottis, (Vantanea).

LITERATURE

On Wood Structure

Benoit 169, Cooper 461, Heimsch 938, Howard 1088, Pereira 1687, Pfeiffer, J. Ph. 1713, Record 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2206, 2207.

✓ 72. MALPIGHIACEAE

(FIG. 65 on p. 270; FIG. 67 on p. 280; FIG. 69 on p. 290; FIG. 91 on p. 402)

SUMMARY

(i) GENERAL

A mainly tropical family of trees, shrubs, or climbers, characterized especially by **hairs** with 1 or 2 more or less horizontal arms, attached to the plant by a long or short vertical stalk. True stellate hairs have been recorded only in *Thryallis*. Large complex **glands**, visible with the naked eye, are often present on the lower side of the petiole, and/or the lower side and margin of the leaf. The **stomata** are rubiaceous. The **mesophyll** of the leaf is dorsiventral or isobilateral, and often contains water-storage cells. The structure of the mesophyll and the distribution of the water-storage cells were found by Dubard and Dop (612) and by Niedenzu (1594) to be of value for the identification of genera and species. Other features confined to the leaves of certain species include: (i) A many-layered epidermis. (ii) Mucilaginous epidermal cells. (iii) Fibre-like cells in the mesophyll. The **petiole**, in transverse sections, exhibits a central, arc-shaped, vascular strand, which is sometimes accompanied by small accessory ones in the latero-superior position. **Crystals** are sometimes solitary, but more frequently clustered; styloids are rare. The **cork** of the young stem is usually superficial in origin, the cells being either thin-walled, or with their inner tangential and, to a less

extent, their lateral walls strongly thickened. **Secretory cells**, whose contents are deeply stained with haematoxylin, are common in the parenchymatous tissues of both leaf and stem. The **pericycle** contains small, isolated groups of fibres, whilst the **xylem** and **phloem** have the form of continuous cylinders traversed by narrow rays in the limited number of species which have been examined. Various types of **anomalous thickening** occur in

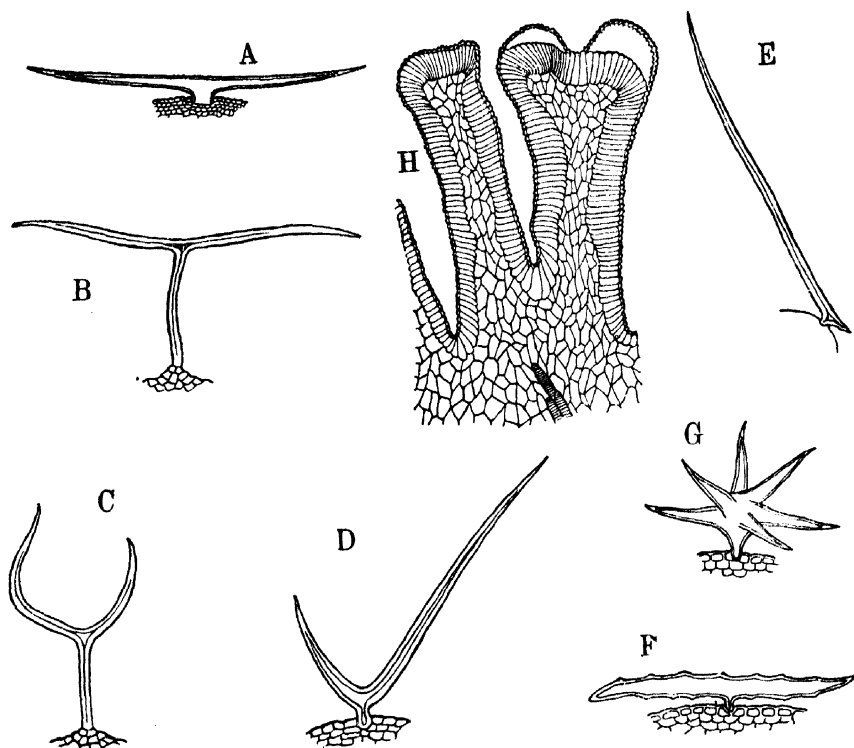


FIG. 67. MALPIGHIACEAE

Hairs of: A, *Malpighia urens* L. B–C, *Peixotoa macrophylla* Griseb. D, *Mascagnia cordifolia* (Juss.) Griseb. E, *Camarea hirsuta* St. Hil. F, *Hiraea chrysophylla* Juss. G, *Thryallis brachystachys* Lindl. H, A piece of the margin of a calyx-gland of *Lophopteris splendens* Juss.—After Niedenzu.

certain members of the family. For instance, the xylem is sometimes furrowed (*Heteropteris*, *Peixotoa*, *Tetrapteris*), or the furrows may become so extensive that the xylem mass is divided into separate portions (*Banisteria*, *Mascagnia*, *Mezia*, *Tetrapteris*). Sometimes a secondary cambium arises in the parenchymatous tissue between the xylem groups (*Stigmaphyllon*). Interxylary phloem is always present in *Dicella* and sometimes in *Stigmaphyllon*.

(ii) Wood

Vessels mostly medium-sized, commonly in radial multiples of 2–3 and sometimes with a definite radial pattern; semi-ring-porous in one species; perforations exclusively simple and intervacular pitting alternate; pits to ray cells mostly small and bordered, but large and simple in a few genera; members

of medium length. **Parenchyma** usually predominantly paratracheal, scanty to confluent, occasionally abundant and banded, diffuse parenchyma sometimes present and occasionally predominant. **Rays** mostly 2-3 cells wide, markedly heterogeneous. **Fibres** with simple pits on the radial walls, often septate; of medium length to moderately long. **Anomalous structure**, see under (i) above.

LEAF

Usually dorsiventral, less frequently isobilateral or centric (for further details see mesophyll). **Hairs** (Fig. 67 A-H) very characteristic, mostly consisting of unicellular trichomes, usually with 2 more or less horizontal arms attached to the plant by a short or long vertical stalk. The 2-armed hairs exhibit modifications in different genera and species, the relative lengths of the arms and the degree of twisting, as well as the smoothness of the external walls being variable characters. Other modifications of the 2-armed trichomes include stinging hairs in certain species of *Malpighia* and bristle hairs in *Camarea*. Stellate hairs confined to *Thryallis*. Large complex sunken or cushion-shaped **glands** common on the petiole as well as on the lower side of the margins of the lamina. Glands with more or less elongated stalks also recorded on the leaf in species of *Aspicarpa* and *Gaudichaudia*. **Epidermis** composed of cells with very small lumina in species of *Hiraea* and *Tetrapteris*; cells sometimes elongated and palisade-like in *Acridocarpus*, *Banisteria*, *Burdachia*, *Byrsonima*, or very large (even wider than the whole of the assimilatory tissue) in certain species of *Camarea*. Very large epidermal cells distributed amongst much smaller ones and sometimes penetrating deeply into the mesophyll occur in species of *Aspidopterys*, *Flabellaria*, *Malpighia*, *Microsteira*, *Pterandra*, *Ryssopterys*, *Spachea*, *Triaspis*, *Tristellateia*. The enlarged epidermal cells sometimes appear as translucent spots in the leaves. Epidermis consisting wholly or locally of 2 or more layers in certain species of *Acridocarpus*, *Banisteria*, *Blepharandra*, *Hiraea*, and *Tetrapteris*; mucilaginous in *Triaspis* sp.; lower epidermis papillose in certain species of *Burdachia*, *Heteropteris*, and *Stigmaphyllon*. **Stomata** nearly always confined to the lower surface except in *Caucanthus edulis* Forsk and *Triaspis* spp.; rubiaceous in all investigated genera except *Diacidia*; guard cells usually elongated to elliptical in surface view.

Mesophyll, according to Solereder, Dubard and Dop (612), and Niedenzu (1598), isobilateral with palisade tissue towards both surfaces or consisting of homogeneous palisade tissue in species of *Acridocarpus*, *Banisteria*, *Byrsonima*, *Dinemagonum*, *Echinopterys*, *Hiraea*, *Microsteira*, *Sphedamnocarpus*, *Stigmaphyllon*, *Tetrapteris*, *Triaspis*, *Tricomaria*, and other related genera. Palisade cells specially tall in species of *Galphimia*, *Heteropteris*, *Stigmaphyllon*; containing little chlorophyll and serving for the storage of water in species of *Diplopterys*, *Galphimia*, *Spachea*. Water-storage cells also recorded at the boundary between the palisade and spongy mesophyll in certain species of *Stigmaphyllon* and *Tetrapteris*; immediately on the inside of both upper and lower epidermis in *Banisteria*, *Janusia*, *Philgamia*, and *Tricomariopsis*; occurring only below the upper epidermis in the region of the veins in *Acridocarpus*; situated at the centre of the lamina in species of *Aspidopterys*, *Caucanthus*, *Flabellaria*, *Microsteira*, *Sphedamnocarpus*, *Triaspis*, where a few

or a large proportion of the mesophyll cells serve as water-storage organs. Individual cells of the outermost layer of palisade tissue also serve for water storage in species of *Aspidopterys*, *Diploteris*, *Tetrapteris*. Water-storage cells are also common around the vascular bundles of the veins. Differences in the structure of the epidermis and mesophyll, as well as in the distribution of water-storage cells, are also stated by Niedenzu (1594) to be of value for the identification of species. Leaf characters have also been used by Dubard and Dop (612) to confirm the existence of affinities between members of the family from America and Madagascar respectively. Vascular bundles of the **veins** sometimes not supported by mechanical tissue, e.g. in species of *Banisteria*, *Heteropteris*, *Spachea*, *Stigmaphyllon*; accompanied by groups of mechanical elements in the phloem in species of *Diploteris* and *Malpighia*; surrounded by a continuous ring of mechanical elements in species of *Acmanthera*, *Coleostachys*, *Dicella*, *Diploteris* (pro parte), *Glandonia*, *Lophopterys*, *Peixotoa*, *Stigmaphyllon*, *Tetrapteris*. A bundle consisting almost entirely of mechanical tissue follows the course of the leaf margin in species of *Heteropteris*, *Malpighia*, and *Tetrapteris*. Cells over the midrib contain abundant **tannin** in *Janusia gracilis* Gray, according to Clausen (431). **Petiole**, in transverse sections, exhibiting a single arc-shaped vascular strand, sometimes accompanied by very small ones in the latero-superior position, in certain species of *Galphimia* (Fig. 65 F), *Heteropteris* (Fig. 65 G), and *Malpighia*, ends of the median vascular arc very much incurved, e.g. in *Hiptage* (Fig. 65 I); the vascular strand accompanied by little or no sclerenchyma in certain species of *Banisteria*, *Galphimia*, *Heteropteris*, *Janusia*, *Malpighia*, *Philgamia*, and *Tricomariopsis*; with, according to Dubard and Dop (612), sclerenchymatous fibres on both sides in *Acridocarpus*. Cells containing a gum-like substance present in the 'cortex' of the petiole in *Heteropteris* sp.

Calcium oxalate present in the form of clustered or solitary **crystals**, those of *Hiraea* and certain species of *Banisteria* especially large; styloids occur in the assimilatory tissue of *Banisteria*, *Janusia*, *Peixotoa*, *Philgamia*, and *Tricomariopsis*. Solitary crystals more frequent in members of the family from the Old World than in American species, but the exact form of the crystals is stated by Niedenzu (1594) to be of very limited taxonomic value.

AXIS

YOUNG STEM (Fig. 65 M)

Cork superficial in origin in certain species of *Byrsonima*, *Galphimia*, *Heteropteris*, and *Malpighia*, but described by Clausen (431) as possibly originating near the endodermis in *Janusia gracilis* Gray; cells thin-walled in *Galphimia gracilis* Bartl. but with strong thickenings on the inner tangential and to a lesser extent on the lateral walls in *Heteropteris chrysophylla* H.B. et K. and *Malpighia* sp. **Cortex** sometimes containing groups of stone cells in *Malpighia*. **Pericycle** including isolated strands of fibres in the few species of *Galphimia* (Fig. 65 M), *Heteropteris*, and *Malpighia* actually examined, but pericyclic sclerenchyma stated to be absent from a few species of *Byrsonima* and *Malpighia*. Primary **phloem** constituting a narrow, closed cylinder; with simple plates to the sieve tubes in *Byrsonima* sp. and *Malpighia* sp.; secondary phloem, including concentric layers of thick-walled, abundantly pitted fibres in certain species of *Byrsonima* and *Malpighia*.

Xylem in the form of a closed cylinder, traversed by narrow rays, in all the species so far examined. Vessels with simple perforations. **Pith** said by Clausen (431) to contain stone cells in *Janusia gracilis*. Clustered **crystals** common in the cortex and phloem; solitary types recorded in *Malpighia* sp. Crystals present in 2-chambered cells in the phloem of *Hiraea* and other genera. **Anomalous structure**, see p. 284.

WOOD (Fig. 69 D-H)

Vessels varying in size from very small (less than $50\ \mu$ mean tangential diameter) in *Malpighia*, *Ptilochaeta*, *Spachea*, *Tetrapodenia*, and *Thryallis* to large (over $200\ \mu$) in some of the lianes, e.g. *Banisteriopsis* and *Stigmaphyllon*. Radial multiples common throughout, with 4 or more per group in all but a few specimens, except for *Heteropteris multiflora* (DC.) Hochr., in which the vessels are all solitary; juxtaposition of the multiples gives a definite radial pattern in *Diacidia*, *Lophanthera*, *Ptilochaeta*, and *Thryallis*, but in *Ptilochaeta* the pattern may also be tangential locally; also with a tendency to clusters in some species, particularly the small vessels of the lianes; mostly between 20 and 40 per sq. mm., fewer in *Bunchosia*, *Byrsonima*, and *Glandonia*, and more numerous in *Malpighia*; semi-ring-porous in *Ptilochaeta* and ring-porous, according to Heimsch (938) in *Galphimia glauca* (Poir.) Cav.; spiral thickening reported in *Peixotoa* (Solereder) and *Tricomaria* (2517). Perforations exclusively simple. Intervascular pitting alternate, typically very small to minute, but moderately large in *Banisteriopsis leptocarpa* R. O. Williams; pits to ray cells generally similar to the intervacular pitting, except in *Burdachia*, *Glandonia*, and *Tetrapodenia*, in which larger simple pits are common; very occasional large simple pits or unilaterally compound pits occur in most of the genera; pits vestured (78). Tyloses present in only a few species; solid deposits present in *Banisteria*, *Malpighia*, and *Stigmaphyllon*. Mean member length 0.4–0.8 mm. **Parenchyma** predominantly paratracheal in most genera, consisting often of only a few cells about the vessels (Fig. 69 F), but sometimes aliform in *Heteropteris* and confluent in *Bunchosia* (Fig. 69 G), *Burdachia*, and *Ptilochaeta*; with some diffuse parenchyma in addition in *Burdachia*, *Lophanthera* (1883), *Ptilochaeta*, *Spachea* (1883), and *Thryallis* (1883); predominantly apotracheal (diffuse or banded) in *Malpighia*, *Tetrapodenia*, and *Triopteris*; in broad bands 4 or more cells wide in *Stigmaphyllon*; obscure or absent from *Glandonia*; terminal in *Diacidia*. Typically filled with dark contents and very commonly containing small to large chambered crystals. Strands of 2–4 cells. **Rays** up to 2–3 (occasionally 4) cells wide; uniseriate or partially biseriate, according to Williams (2430) in *Spachea tricarpa* A. Juss.; less than 1 mm. high, except in *Burdachia*, *Thryallis*, and *Triopteris*; uniseriates few to numerous, composed of square to upright cells; usually 6–12 rays per mm., but sometimes more numerous; very distinctly heterogeneous (Kribs's Type I and II A) with 2 or 3 marginal rows of large upright cells and with 4 or more rows in *Burdachia*, *Glandonia*, *Heteropteris*, and *Malpighia*. Occasionally less markedly heterogeneous (Kribs's Type II B), according to Heimsch, and sometimes only weakly heterogeneous in *Bunchosia* (1886). Cells characteristically filled with a dark substance and often containing crystals in ordinary or chambered cells, and in idioblasts in *Bunchosia* and *Burdachia*. **Fibres** with simple pits, more numerous on the radial than on the

tangential walls; septate in *Banisteria*, *Byrsonima*, *Glandonia*, *Ptilochaeta*, and *Tetrapteris*, and, according to Solereder, in *Hiraea* and according to Heimsch (938), with some septate fibres in *Heteropteris* and *Spachea*; Heimsch refers also to the common occurrence of gelatinous fibres; commonly containing gum; walls moderately thick to thick. Mean length 1.0–1.8 mm.

ANOMALOUS STRUCTURE (Fig. 91 D)

Interxylary phloem present in all species of *Dicella* and in *Stigmaphyllon* sp.

In young stolons of *Dicella nucifera* Chod. the structure is normal. At a later stage some of the cells cut off from the cambium towards the inside fail to differentiate as xylem elements, but form blocks of parenchyma in which sieve tubes develop. More xylem is then differentiated externally to the abnormal phloem, so that the latter becomes isolated as islands in the xylem. Successive islands of interxylary phloem are formed in the same way as the stem grows older.

The root of the same species exhibits the same type of anomalous structure as the stem, but becomes locally swollen into ellipsoid or fusiform tubercles, 5–10 cm. long \times 3–4 cm. broad. The tubercles are composed mainly of parenchyma, with groups of fibres embedded in it. They are stated by Chodat and Vischer (399) to contain inulin and secretory cells with brown contents.

The xylem is at first normal in structure and mode of development in *Stigmaphyllon*, but it contains abundant parenchyma and ray tissue in which cambial layers are subsequently laid down, and give rise to new bundles of xylem and phloem.

Certain lianes belonging to this family are characterized by a lobed mass of xylem, or one which becomes lobed during development, e.g. in *Heteropteris*, *Peixotoa*, *Tetrapteris* (Fig. 91 D); subsequent enlargement of the tissue between the xylem radii sometimes causes the xylem to become split up into groups in *Banisteria*, *Mascagnia*, *Mezia*, and *Tetrapteris*. For further particulars see Solereder, Pfeiffer (1712), and Chodat and Vischer (399).

Lianes belonging to the genera *Heteropteris* (pro parte), *Hiptage*, *Schwannia*, *Tetrapteris* (pro parte), and *Thryallis* are stated to be normal in structure.

TAXONOMIC NOTES

Heimsch (938) points out that the Malpighiaceae have a more highly specialized wood structure than the Linaceae, Humiriaceae, and Erythroxylaceae, with which they are often associated, and that this family and the Vochysiaceae, though showing indications of relationship to these families and to the Polygalaceae, Tremandraceae, Trigoniaceae, and Zygophyllaceae, differ from all of them, particularly in having vested vessel pits and simple-pitted fibres.

ECONOMIC USES

According to Perrot and Raymond-Hamet (1698), the anatomical structure of a Brazilian plant which is capable of inducing a state of intoxication, pleasant dreams, and other hallucinations, and of which the local names are Yagé, Ayahuasco, and Caapi, suggests that it is a species of *Banisteria*. The

bark of certain species of *Byrsonima* is used in tanning. Many of the woods have an attractively variegated colour, but few of the trees are large enough to be important sources of timber. Some species of *Byrsonima* are large trees and produce timber that is used for various purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acmanthera, Acridocarpus, Aspicarpa, Aspidopterys, Banisteria, Blepharandra, Burdachia, Byrsonima, Camarea, Caucanthus, Coleostachys, Diacidia, Dicella, Dinemagonum, Diploterys, Echinopteris, Flabellaria, Galphimia,* Gaudichaudia, Glandonia, Heteropteris,* Hiptage,* Hiraea, Janusia, Lophopterys, Malpighia,* Mascagnia, Mezia, Microsteira, Peixotoa, Philgamia, Pterandra, Ryssopterys, Schwannia, Spachea, Sphedamnocarpus, Stigmaphyllon, Tetrapteris, Thryallis, Triaspis, Tricomaria, Tricomariopsis, Tristellateia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Banisteria, Bunchosia, Burdachia, Byrsonima, Diacidia, Glandonia, Heteropteris, Lophanthera, Malpighia, (Peixotoa), Ptilochaeta, Spachea, (Stigmatophyllon), Tetrapodenia, Tetrapteris, Thryallis, (Tricomaria), Triopteris.

LITERATURE

(i) On General Anatomy

Chodat and Vischer 399, Clausen 431, Dubard and Dop 612, Niedenzu 1594, 1598, O'Donnell and Lourteig 1631, Perrot and Raymond-Hamet 1698.

(ii) On Wood Structure

Bailey 78, Benoist 170, Chalk and Chattaway 358, Cozzo 2517, Heimisch 938, Kribs 1283, Pfeiffer, H. 1712, Pfeiffer, J. Ph. 1713, Record 1815, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2207, Williams 2430.

✓ 73. ZYGOPHYLLACEAE

(FIG. 65 on p. 270; FIG. 68 on p. 286; FIG. 69 on p. 290)

SUMMARY

(i) GENERAL

A tropical and sub-tropical family of shrubs or somewhat woody herbs with hairy, fleshy, or leathery leaves. Certain species of *Kallstroemia*, *Tribulus*, and *Zygophyllum* are annuals. The Zygophyllaceae and Thymelaeaceae are said to be the only families poisonous to camels. The **hairs** are usually unicellular and simple, but more rarely unicellular and 2-armed. The **mesophyll** of the leaf is generally centric, and partly composed of water-storage cells in certain species. The vascular bundles of the leaf **veins** are sometimes surrounded by a sheath of thin or thick-walled parenchymatous cells which may contain chlorophyll. The **petiole**, in transverse sections, exhibits a central vascular strand which is somewhat complex in structure, and therefore variable in appearance in sections taken at different levels within a single

petiole. In most instances the central strand has the form of a closed or somewhat interrupted cylinder. Two or more subsidiary strands also occur in the latero-superior position. The primary **cortex** of the axis is usually composed of thin-walled parenchyma in which stone cells are sometimes embedded. The **pericycle** is generally characterized by separate strands of fibres, between which stone cells are sometimes present. The **phloem** and

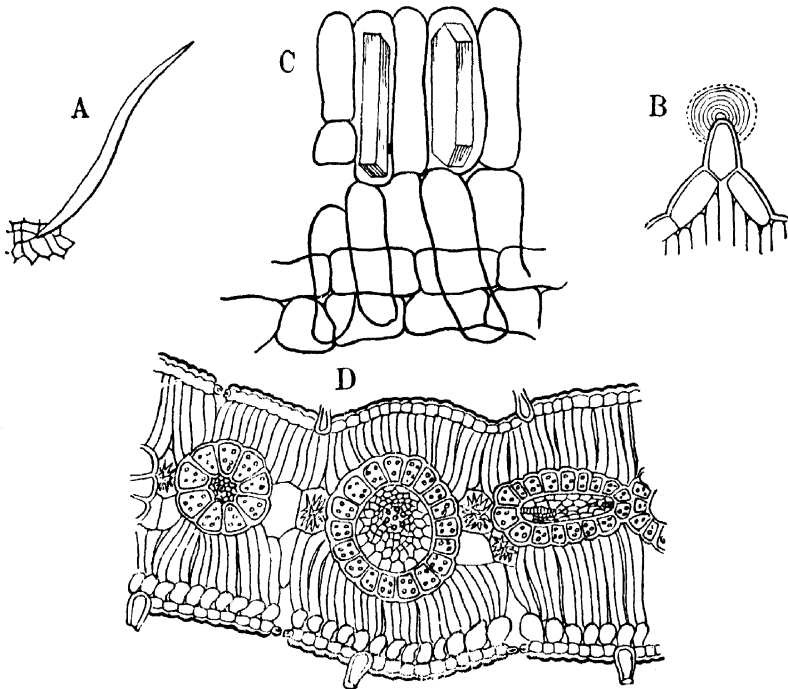


FIG. 68. ZYGOPHYLLACEAE

A, Hair of *Larrea divaricata* Cav. B, Glandular hair of *Fagonia arabica* L. C, Crystal-cells from the phloem of *Guaiacum officinale* L. D, Transverse section of the leaf of *Tribulus alatus* Del.—A, By Solereder; B and D after Volkens; C after Möller.

xylem in the internodes of the young stem constitute closed cylinders surrounding the pith, or the xylem may be interrupted by broad primary medullary rays. **Crystals** are mostly clustered, but sometimes solitary. Styloids are especially characteristic of the phloem of certain species of *Guaiacum*, *Larrea*, and *Porlieria*.

(ii) Wood

The most striking characters of the woods are the storying of all the elements and the high number of stories per mm. (8–17), the predominance of fusi-form parenchyma cells, very small intervacular pitting, and the occurrence of tracheids. With the exception of *Balanites*, which has large unstoried rays and no crystals, other characteristic features are narrow, low rays and abundance of crystals in the parenchyma and sometimes in the rays. **Vessels** very small to moderately large, exclusively solitary or with oblique radial

pattern or in large clusters, perforations simple, intervacular pitting alternate; members very to extremely short. **Rays** all narrow, short, and storied or all large and not storied; homogeneous. **Parenchyma** usually typically apotracheal, diffuse or in uniseriate bands. **Fibres** with bordered pits, the borders moderately distinct to indistinct; with thick walls, usually storied; of medium length in *Balanites*, very to extremely short in the other genera. **Vasicentric tracheids** usually present.

LEAF

Usually dorsiventral, but centric in certain genera (see 'Mesophyll' below). **Hairs** mostly simple and unicellular (Fig. 68 A), either with thick walls and narrow lumina or with thin walls and relatively wide lumina; more rarely unicellular but 2-armed, this type occurring especially in the *Agrophyllum* section of *Zygophyllum*. A dense clothing of procumbent unicellular hairs has been recorded in species of *Bulnesia*, *Chitonina*, *Kallstroemia*, *Sericodes*, *Tribulus*, *Viscainoa*. Glandular hairs common on small elevations of the leaf surface in *Fagonia* (Fig. 68 B) and glands with a clavate or spherical head in *Peganum harmala* Linn. The whole surface of the leaf is covered with **mucilage glands** in *Zygophyllum fabago* Linn. according to Cunningham (515). The **resinous substances** covering the surface of *Neoschroetara tridentata* (DC.) Briq. (syn. *Larrea mexicana* Moric) are stated to be secreted from the epidermis of the stipules and not from external glands. Cells of the **epidermis** usually provided with a thick cuticle; polygonal in surface view in certain species of *Guaiacum*, *Larrea*, *Porlieria*, and *Zygophyllum*. Every epidermal cell contains a crystal in *Guaiacum officinale* Linn. **Stomata** generally present on both surfaces, but more numerous on the lower side, either sunk or raised above the level of the epidermis; ranunculaceous. Sunken stomata recorded especially in the leathery leaves of species of *Bulnesia*, *Guaiacum*, *Neoschroetara*, *Pintoa*, *Porlieria* and in the fleshy leaves of *Zygophyllum*. Small **black dots**, each consisting of a few large thin-walled cells lying under the epidermis and accompanied by a few cells of the epidermis itself with brownish contents, present in *Pintoa chilensis* Gay. **Hypoderm** recorded beneath the upper epidermis in *Peganum harmala*. **Mesophyll** centric in certain species of *Guaiacum*, *Larrea*, *Nitraria*, *Porlieria*, *Seetzenia*, *Tribulus* (Fig. 68 D), and *Zygophyllum*; containing scattered mucilage cells in certain species of *Nitraria*, and tanniniferous idioblasts in two species of the same genus. Lowermost cell layer of the mesophyll consisting of colourless water-storage cells in certain species of *Tribulus*; central portion of the cylindrical leaf consisting of aqueous tissue in *Zygophyllum simplex* Linn. Mesophyll containing spicular fibres branching off from the sclerenchyma of the veins and sometimes extending to the epidermis in *Nitraria* sp. Vascular bundles of the **veins** enveloped by sheaths of pitted cells with fairly thick walls in *Tribulus* spp. (Fig. 68 D) and *Zygophyllum* sp. according to Sabnis (1977) and Solereder, and by sheaths of thin-walled cells in *Balanites roxburghii* Planch. and *Fagonia* sp. Sheaths absent from around the veins in *Seetzenia* sp. **Petiole**, in transverse sections, exhibiting a central ring of vascular bundles in *Bulnesia*, *Fagonia*, *Guaiacum*, *Larrea*, *Porlieria*, *Tribulus*, but closed vascular cylinders also recorded or observed in *Guaiacum* (Fig. 65 D)

and in *Zygophyllum*; the central strand is accompanied by 2 or more lateral bundles in all of the species examined. The course of the bundles is somewhat complex in the petiole owing to splitting and fusion, the degree of separation of the strands in the central ring therefore varying in sections taken at different levels. The main vascular strand of the petiole has the form of a continuous cylinder accompanied by groups of pericyclic fibres similar to those of the axis in *Guaiacum* and *Zygophyllum* when observed in transverse sections through the distal end. Two subsidiary vascular strands also present in a latero-superior position in the same 2 genera. Petiole of *Balanites aegyptiaca* (L.) Delile with a circle of closely approximated but individually distinct bundles surrounding a large, collateral, medullary strand. Leaves of *Zygophyllum stapfi* Schinz become detached from the plant in periods of drought according to Zemke (2505). **Crystals** usually clustered, the clusters being very large in *Balanites aegyptiaca*, solitary ones more frequent in the axis; acicular crystals recorded in the leaf tissue of *Nitraria* sp. and *Peganum harmala* Linn. and raphide sacs in *Peganum crithmifolium* Eichw. A single crystal said to occur in every epidermal cell in *Guaiacum officinale*. Crystalline masses recorded in the cells of *Fagonia* and in the intercellular spaces of *Nitraria* and *Zygophyllum*, these being especially characteristic of species growing on saline soils.

AXIS

YOUNG STEM (Fig. 65 E)

Epidermis composed of cells with very thick cuticle on the outer walls in *Guaiacum officinale* Linn. and *Balanites aegyptiaca* (L.) Delile. **Stomata** in the last of these species situated in deep pits. **Cork** arising in the epidermis or sub-epidermis in most species, but originating on the inside of the strands of pericyclic fibres in *Fagonia cretica* Linn.; usually strongly developed. Primary **cortex** consisting of aqueous tissue in *Tribulus* sp. and *Zygophyllum*; the broad cortex of *Augea capensis* Thunb. is composed of thin-walled parenchyma according to Schonland (2047). Stone cells present in the cortex of species of *Balanites* and *Bulnesia*, and stone cells and, according to Cunningham (515), sclereids at the nodes of *Zygophyllum fabago* Linn. Bundles of fibres were observed in the primary cortex as well as in the pericycle of *Z. fabago* grown at Kew. **Pericycle** containing well-defined, isolated strands of fibres in *Augea*, *Balanites*, *Fagonia*, *Guaiacum* (Fig. 65 E), *Seetzenia*, *Tribulus*, and *Zygophyllum*; the fibre strands stated by Cunningham (515) to be interrupted at the nodes in *Zygophyllum fabago*. Pericycle containing a composite and continuous ring of sclerenchyma in *Balanites aegyptiaca* and *Peganum*. **Xylem** and **phloem** forming closed cylinders in the internodes of *Guaiacum* and *Zygophyllum*, but the xylem is said to consist of a composite cylinder of closely placed bundles in certain species of *Balanites*, *Fagonia*, *Seetzenia*, and *Tribulus*. Vessels usually small (radial diameter seldom more than $30\ \mu$ in *Guaiacum officinale*, but attaining $60\ \mu$ in *Balanites aegyptiaca*), mostly solitary, but sometimes tending to be in radial rows. Vessels with simple perforations. **Pith** consisting of thin-walled cells in *Fagonia*, *Tribulus*, *Zygophyllum* (very large and becoming hollow in *Z. fabago*); containing stone cells in *Guaiacum*. **Crystals** mostly solitary or clustered; styloids recorded in the phloem of *Guaiacum officinale* (Fig. 68 c), *Neoschroetera tridentata* (DC.)

Briq. (syn. *Larrea mexicana* Moric); small acicular crystals present in the phloem of *Nitraria schoberi* Linn. and in the epidermis, primary cortex, phloem, and rays of *Peganum harmala* Linn. Large **mucilage cavities** recorded in the primary cortex and secondary phloem of *Nitraria* sp. crystals sometimes being deposited in them as well.

WOOD (Fig. 69 I-M)

Vessels medium-sized (mean tangential diameter 100–200 μ) in *Balanites* and *Guaiaacum*, very small to moderately small (50–100 μ) in the other genera; solitary in *Guaiaacum*, *Larrea*, *Nitraria* (1493), and *Porlieria*, but with a few multiples in *Bulnesia* and *Sericodes* (938) and in large clusters, mostly of solitary vessels, in *Balanites*; with a radial or oblique pattern in *Bulnesia*, *Nitraria* (1493), *Plectrocarpa* (495), and *Porleiria* and sometimes in *Balanites*; varying in number from fewer than 5 per mm. in *Balanites* to more than 70 per mm. in *Larrea*; tending to be ring-porous in some species of *Bulnesia* and *Plectrocarpa* (495). Perforations exclusively simple. Intervascular pitting alternate, very small and numerous; pits to ray cells similar to the intervascular pitting (absent from *Balanites* as the vessels do not touch the rays). Vessels commonly filled with gummy or resinous deposits, except in *Balanites*. Mean member length 0.07–0.2 mm. **Parenchyma** predominantly apotracheal in *Balanites*, *Larrea*, *Plectrocarpa*, and *Porlieria*, diffuse and in numerous, irregular, uniseriate bands; similar parenchyma present, and sometimes predominant, in *Guaiaacum* but often tending to be associated with the vessels abaxially and sometimes accompanied by narrow aliform wings (Fig. 69 M); almost entirely paratracheal in *Bulnesia* and *Nitraria* (1493); apparently terminal bands sometimes present. Storied; usually with 8–11 stories per mm., but according to Cozzo (495), commonly with 14, and up to 17 stories per mm. in *Plectrocarpa*. Fusiform cells very common, and sometimes almost the only type of parenchyma present apart from crystalliferous strands; crystals present, except in *Balanites*; in idioblasts in *Larrea* and in chambered cells in *Bulnesia*, *Guaiaacum*, and *Porlieria*. Markedly disjunctive and with conspicuously grouped pits. **Rays** (except in *Balanites* and *Bulnesia retama* (Gill.) Gris. and *Nitraria* (1493)), small, 1–2 cells wide, exclusively uniseriate in some species of *Guaiaacum*, *Porlieria*, and *Sericodes* (938); exceptionally low, not more than 8 cells high and commonly not more than 4–6; storied, 10–11 stories per mm.; according to Cozzo (495), the rays in 1 species of *Plectrocarpa* are up to about 3 cells wide, commonly more than 1 story high and themselves not storied; homogeneous (Kribs's Types II and III), except in *Larrea*, which has single marginal rows of square cells. In *Bulnesia retama* and *Nitraria* the rays are reported (1493, 1886) to be up to 3 and 3–4 cells wide respectively and 30 cells high. In *Balanites* the rays are all broad (uniseriate rays absent), up to 20 cells wide and 1.7 mm. high, and with sheath cells. **Fibres** with distinctly bordered pits, which are more numerous in the tangential than the radial walls, in *Balanites*; pits in the other genera with moderately distinct (*Larrea*) to indistinct borders. Heimsch (938), however, states that the fibrous elements are in most cases tracheids and seldom fibre-tracheids. Storied except in *Balanites*. Walls thick. Mean length about 1.0 mm. in *Balanites*, 0.35–0.6 in the other genera. **Vasicentric tracheids** typically present, but not observed in *Porlieria*.

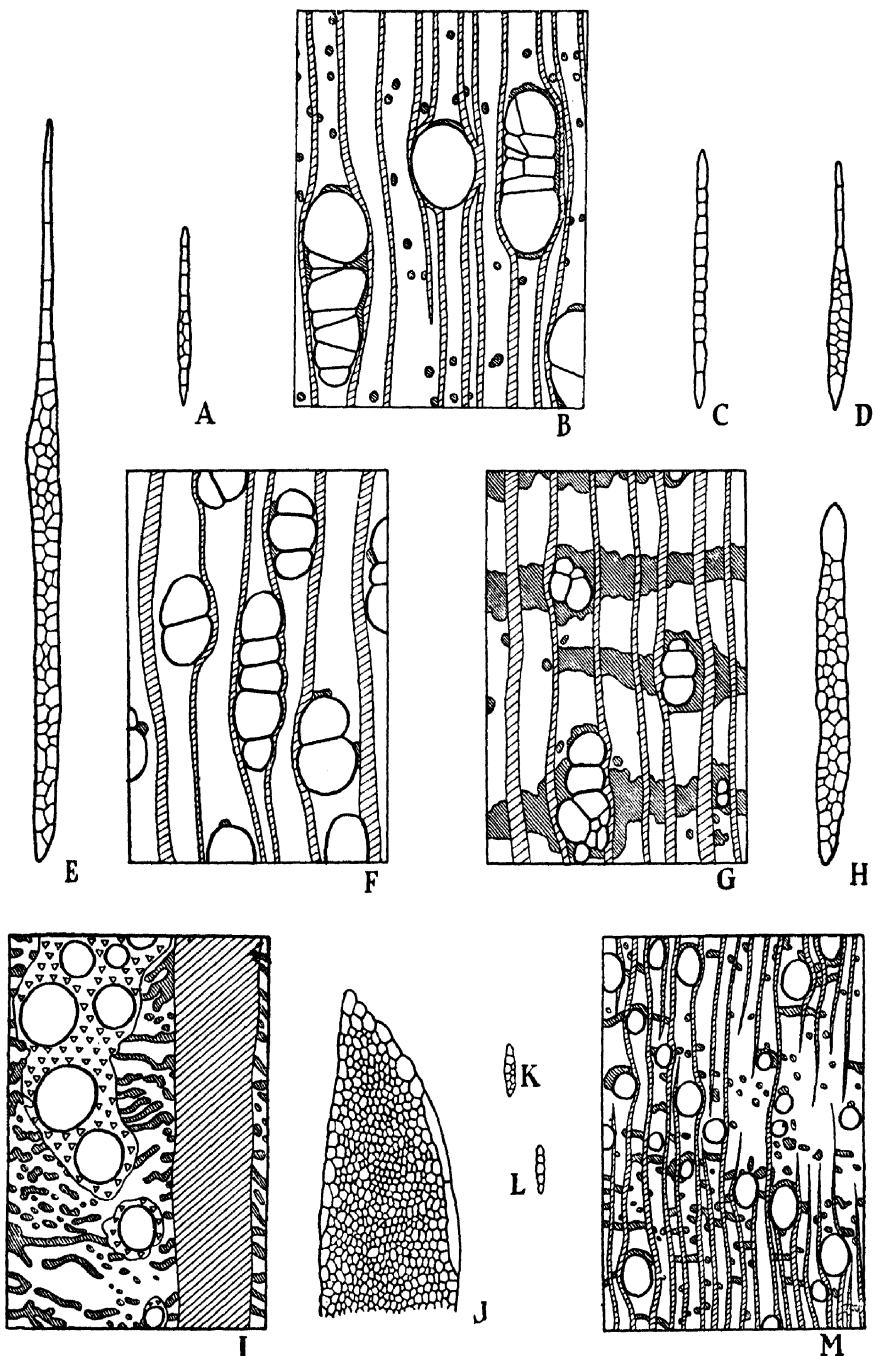


FIG. 69. OXALIDACEAE, A-C; MALPIGHIACEAE, D-H; ZYGOPHYLLACEAE, I-M

A, *Connaropsis griffithii* Planch. B, *C. griffithii* Planch. C, *Averrhoa carambola* Linn. D, *Ptilochaeta nudipes* Griseb. E, *Glandonia macrocarpa* Griseb. F, *Byrsomima coriacea* (Sw.) Korth. var. B. G, *Bunchosia cornifolia* H. B. et K. H, *B. cornifolia* H. B. et K. I, *Balamites aegyptiaca* Del. J, *B. aegyptiaca* Del. K, *Bulnesia arborea* Engl. L, *Guaiacum officinale* Linn. M, *G. officinale* Linn.

ROOT

Primary structure diarch in *Fagonia*, *Tribulus*, and *Zygophyllum*, but triarch in *Guaiaacum* and *Porlieria*.

Tubercles of two distinct sizes, somewhat resembling the bacterial nodules of the Leguminosae, and infested both externally and internally by fungal hyphae, recorded by Issatschenko (1125) in *Tribulus terrestris* Linn. and by Sabet (1976 A) in *Fagonia*, *Tribulus*, and *Zygophyllum*. The root structure of *Tribulus cistoides* Linn. is described under 'Economic Uses'.

TAXONOMIC NOTES

Balanites. Record (1786) states that the wood structure of *Balanites* bears no resemblance to that of *Bulnesia*, *Guaiaacum*, and *Porlieria*. Though strikingly different owing to its large rays and clustered pores, it has many less obvious, but not necessarily less significant, features in common with these genera, e.g. vasicentric tracheids, small vessel pitting, fibres with thick walls and bordered pits, distribution of parenchyma, abundance of fusiform parenchyma cells, storying of elements other than the rays and the number of stories per mm.

Heimsch (938) considers that, apart from the rays, the wood anatomy of *Balanites* suggests affinity with the Zygophyllaceae rather than with the Simarubaceae. Elsewhere, however, he states that 'the high and wide rays of *Balanites* may be evidence from a structural point of view for excluding this genus from the Zygophyllaceae which otherwise have only low, and narrow rays'.

The woods of the family form a very distinctive, natural group, and must be regarded as highly specialized. They are remarkable for their combination of several highly specialized features, such as a vessel member length of 0.1–0.2 mm., storied structure, homogeneous rays and fusiform parenchyma cells, with several other features, such as solitary vessels, diffuse parenchyma and fibres with bordered pits, which are usually associated with an unspecialized structure.

ECONOMIC USES

The only important timber from this family is the Lignum Vitae, *Guaiaacum officinale* Linn. from the western Indies and South America. This timber has long been known to commerce; one of its principle uses is for the bearings or bushing blocks for lining the stern tubes of the propellor shafts of steamships, for which the self-lubricating properties of the wood, owing to its resin content, make it especially suitable. Other uses include bowling balls, mallets, and pulley sheaves. *Guaiaacum* resin, used in medicine, is formed chiefly in the cells of the medullary rays of the same species and of *G. sanctum* Linn.

The twigs of the Creosote Plant *Neoschroetera tridentata* (DC.) Briq. (syn. *Larrea mexicana* Moric.) yield a resinous substance used locally in the treatment of rheumatism.

The root of *Tribulus cistoides* Linn. possesses medicinal properties. Transverse sections of the roots of this species 1 cm. thick exhibit, according to Diepenbrock (587), a yellow central cylinder clearly demarcated from the surrounding white tissues. Vessels tending to be in radial rows, and accompanied by tracheids and thick-walled parenchyma. Groundwork of the xylem

composed of fibres. Rays mostly uniseriate, but sometimes partly or wholly 2 or more cells wide. Wood surrounded by cambium and phloem, the latter consisting of a cylinder of small, unthickened, starch-free cells. Large masses of fibres are present externally to the phloem with extensions of the rays between them. Cortex represented by a narrow band of starch-containing cells, bounded externally by several layers of cork cells.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Augea, Balanites,* Bulnesia, Chitonia, Fagonia, Guaiacum,* Kallstroemia, Larrea, Neoschroetera, Nitraria, Peganum, Pintoa, Porlieria, Seetzenia, Sericodes, Tribulus, Viscainoa, Zygophyllum.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Balanites, Bulnesia, Guaiacum, Larrea, (Nitraria), (Plectrocarpa), Porlieria, (Sericodes).

LITERATURE

(i) On General Anatomy

Cunningham 515, Diepenbrock 587, Engler 639, Evenari (Schwarz) 665, Issatschenko 1125, Sabet 1976 A, Sabnis 1977, Schonland 2047, Zemke 2505.

(ii) On Wood Structure

Burgerstein 312, Cozzo 495, Foxworthy 705, Heimsch 938, Howard 1088, Jones 1191, Kanehira 1209, Messeri 1493, Record 1781, 1783, 1786, 1809, 1818, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Wallis 2348.

✓ 74. GERANIACEAE

(FIG. 70 on p. 296)

SUMMARY

(i) GENERAL

A mainly herbaceous family which occurs chiefly in temperate regions. It also includes succulent and shrubby species. The genera described are fairly homogeneous in structure, the greatest differences being between herbs and shrubs. The desert genus *Sarcocaulon* has a highly specialized structure in relation to its habitat. The **hairs** consist either of simple, unicellular and uniseriate types or they may be glandular. The oil secreted by the glandular hairs is highly scented and sometimes distilled for use in perfumery. The odour which is usually associated with *Geranium* is due to these oils. Tannic acid is also common in the tissues, notably in *Pelargonium* as well as in species of *Erodium* and *Monsonia* from the Egyptian desert. **Crystals** solitary or clustered. The **stomata** are ranunculaceous. The **pericycle** in the axis of *Erodium*, *Geranium*, and *Pelargonium* usually contains a well-defined, continuous ring of sclerenchyma, which is sometimes composite, especially in *Erodium*. The **vascular bundles** in the stem of herbaceous species are usually widely separated and individually distinct, arranged in 1 or sometimes in 2 rings according to the species. The inner bundles tend to be medullary

in certain species of *Geranium*. In some species the phloem of the outer bundles abuts directly on to the sclerenchyma of the pericycle, whilst in other species, such as *Geranium pratense* Linn., inwardly directed sclerenchymatous projections serve to connect the phloem groups of the individual bundles with the main sclerenchymatous ring. The **xylem** and **phloem** form closed cylinders in mature stems of shrubby species owing to the development and activity of interfascicular cambium. The vessels have simple perforations, and the wood fibres are provided with simple pits. The **root** exhibits peculiar thickening ridges in the sub-epidermis of many species of *Erodium*, *Geranium*, and *Pelargonium*.

(ii) WOOD

Vessels with simple or rare multiperforate plates and alternate to opposite pitting. **Parenchyma** scanty paratracheal. **Rays** often absent. **Fibres** commonly septate.

LEAF

Hairs simple, unicellular (*Viviania marifolia* Cav.) or uniseriate; glandular types with uniseriate stalks of varying length and unicellular, spherical heads in *Erodium*, *Geranium*, *Monsonia*, *Pelargonium*, *Viviania*, and *Wendtia*; glandular shaggy types with long multiseriate stalks and multicellular knob-shaped heads in *Biebersteinia*. **Glandular leaf teeth** occur in *Geranium robertianum* Linn. Glandular hairs, where present, secreting oils. Cells of the upper **epidermis** described by Evenari (665) as having thin outer walls and cuticle in *Erodium glaucophyllum* Ait.; those of *Sarcocaulon* found by Planchon (1728) and Zemke (2505) to be unequal in size and to contain chlorophyll. Epidermis of *Monsonia heliotropioides* Boiss., according to Sabnis (1977), papillose especially on the lower surface. **Stomata** present on both surfaces or confined to the lower side according to the species; ranunculaceous. Stomata situated in grooves on either side of the principal vein on the lower side of the leaf in *Balbisia microphylla* Phil.; present in equal numbers on both surfaces in *Pelargonium coronopifolium* Jacq. although the leaf is deeply furrowed only on one side owing to the margins being revolute. **Mesophyll** isobilateral in *Erodium glaucophyllum* Ait. and *Monsonia heliotropioides* Boiss. Vascular bundles of the **veins** said by Legault (1342) to be surrounded by an endodermis in *Erodium* and *Geranium*. Larger veins vertically transcurrent in *Monsonia heliotropioides* Boiss. **Petiole** exhibiting a circle of separate vascular bundles in transverse sections through the distal end in *Biebersteinia*, *Erodium*, *Geranium* (Fig. 70 c), and *Monsonia*. An outer circle of about 14 relatively small bundles and an inner circle of 5 larger ones recorded in *Geranium anemonifolium* L'Hérit. Xylem groups of the bundles almost surrounded by phloem in *Geranium phaeum* Linn., but this character is less pronounced in *G. pratense* Linn. Phloem groups bounded externally by caps of fibres in the pericyclic region, the latter connected by interfascicular sclerenchyma so as to form a ring in some species, e.g. in *Geranium robertianum* Linn. and *Pelargonium zonale* (L.) Ait., but interfascicular sclerenchyma poorly developed in other species, e.g. *Geranium phaeum* Linn., or absent, e.g. in *Geranium pyrenaicum* Burm. f. and *Erodium moschatum* (L.) Hér. Petiole structure of *Pelargonium* (Fig. 70 F) very similar to that of *Geranium*,

but the ring of bundles encloses a large, central medullary strand in many species. For details of petiolar structure in *Pelargonium zonale* (L.) Ait. var. *Meteor* see Doyle's (609) article. A single arc-shaped strand flanked on either side by a smaller bundle occurs in the distal end in *Viviania petiolata* Hook. et Arn. and a solitary but well-developed strand in *Rhynchotheca* and *Wendtia*. **Crystals** solitary or clustered, sometimes situated in idioblasts in *Erodium*; styloids in *Rhynchotheca*; sphaerocrystalline masses in *Erodium* and *Monsonia*; short rows of cells containing cluster crystals in *Wendtia*.

AXIS

STEM (Fig. 70 A, D, J, and K)

Cork originating in the hypodermis, and consisting of cells with wide lumina and thin walls in *Monsonia*. **Cortex** usually rather narrow, bounded internally by a closed, but often composite (especially in *Erodium* (Fig. 70 D)) ring of mechanical tissue representing the **pericycle**. Vascular bundles of *Erodium moschatum* (L.) Hér. each provided with a cap of pericyclic fibres which are smaller in diameter than those of the arcs of interfascicular sclerenchyma which unite the fibre caps of the bundles so as to form a continuous ring. The width of the ring of mechanical tissue varies in different species. Pericycle containing isolated groups of fibres in certain species of *Monsonia*. **Endodermis** conspicuous in young stems of *Geranium pratense* Linn. **Vascular bundles** usually widely separated (Fig. 70 D and K), arranged in 1 or sometimes in 2 more or less distinct rings according to the species, the inner ones said by Solereder sometimes to be inversely orientated. The inner bundles, where present, are larger than the outer ones. Bundles arranged in a single ring in *Geranium phaeum* Linn.; in 2 more or less distinct circles, but connected by sclerenchymatous tissue to the mechanical ring, e.g. in the pericycle of *G. dissectum* Linn., *G. lucidum* Linn., and *G. macrorrhizum* Linn.; in a single ring when young, but the inner bundles become embedded in the pith with increase of age, e.g. in *G. collinum* Steph. and *G. pratense* Linn.; inner bundles free in the pith, outer ones connected with the sclerenchyma ring in *G. robertianum* Linn. Stem structure in *Erodium* and the herbaceous species of *Pelargonium* similar to that of *Geranium*, but the xylem and phloem form closed cylinders in the shrubby species of *Pelargonium* (Fig. 70 J) owing to the formation and activity of an interfascicular cambium. Vessels, except in the protoxylem with spiral thickening, provided with horizontal bordered pits; perforations usually simple, but reticulate types recorded in *Pelargonium* (Thompson 2254). Wood fibres with simple pits except in *Viviania*. **Pith** consisting of thin-walled parenchyma; becoming hollow in certain species.

WOOD¹

Vessels solitary and in multiples and clusters, and often, especially in *Geranium*, confined to radial strips; sometimes ring-porous; with spiral thickening in *Balbisia*. Perforation plates typically simple, but occasional multiperforate plates (ephedroid, reticulate, and scalariform) have been observed (1408, 2254) in *Pelargonium*. Intervascular pitting predominantly alternate, but usually with some transitional and opposite types; pits to ray and wood parenchyma cells large and elongated. **Parenchyma** paratracheal,

¹ Based mainly on the description given by Heimsch (938).

scanty. **Rays**, when present, heterogeneous and very variable in height and size of cell. Absent from some species of *Balbisia*, *Monsonia*, *Viviana*, and *Wendtia*, and, according to Barghoorn (139), from the early formed wood of *Geranium tridens* Hbd., though high-celled multiseriate rays develop later. **Fibres** with simple or indistinctly bordered pits; often septate; walls thin except sometimes in *Balbisia*.

RHIZOME

Endodermis and **pericycle** not well defined in *Geranium maculatum* Linn. according to Holm (1026) but with a single, somewhat excentric ring of **vascular bundles** with interfascicular cambium between them.

ROOT

A characteristic network of **thickening ridges** recorded in *Erodium*, *Geranium*, and *Pelargonium* by Solereder, Holm (1026), and Scott and Whitworth (2074). These thickenings appear to be lignified when tested with phloroglucin and hydrochloric acid or with aniline sulphate, but respond to cellulose reagents after treatment with Schultze's macerating fluid. Fatty acids have been detected in them as well.

SARCOCAULON

The stem of *Sarcocaulon*, a frutescent plant from desert regions in South-west Africa, which bears thorns formed from the petioles after the lamina falls off at the end of the rainy season, is so specialized in structure that the following separate description, based on the accounts by Knuth (1255), Planchon (1728), and Zemke (2505), is given.

Stem covered by a yellow, elastic inflammable layer of **cork**, easily detached from the central tissues, and consisting of several layers of cells filled with resinous contents. The cork serves as an hermetically sealed covering during dry weather (cf. the similar cork in certain species of *Kalanchoe* (family Crassulaceae) from Madagascar). **Cortex** represented by a zone of parenchymatous tissues containing chlorophyll and crystals of calcium oxalate, a special form of starch (not stained readily by iodine) and resinous substances. **Pericycle** demarcated by a few fibres situated externally to the phloem. **Phloem** in radially arranged groups, separated by fairly broad, medullary rays 4-6 cells wide. Ray cells filled with starch, a few cluster crystals of calcium oxalate, and resinous fragments. **Xylem** containing numerous vessels of small diameter. **Pith** similar in structure to the cortex.

TAXONOMIC NOTES

The family constitutes a homogeneous group except for the specialized desert plant *Sarcocaulon*, in which the rather different structure has evidently been evolved in response to the arid conditions in which the plant grows.

Heimsch (938) has pointed out the similarity between the woods of this family and those of the Oxalidaceae, particularly the tendency to elimination of rays, the scanty paratracheal parenchyma and the common occurrence of septate fibres.

MacDuffie (1408) used the structure of the perforation plates of *Pelargonium* to illustrate his argument against the hypothesis that the types of vessels in the Gnetales and the angiosperms are distinct in their mode of derivation.

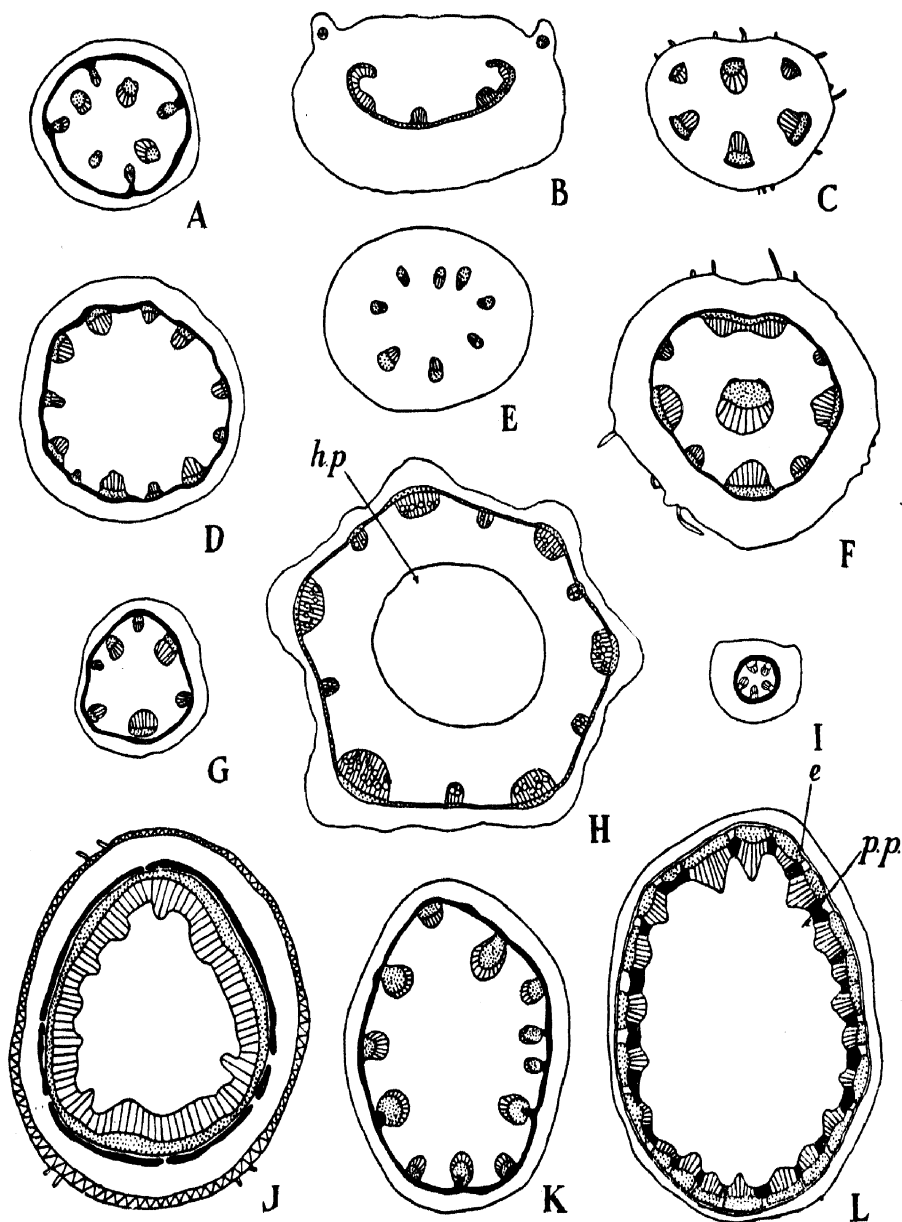


FIG. 70. *GFRANIACEAE*, A, C-D, F, and J-K; *BALSAMINACEAE*, B and H;
TROPAEOLACEAE, E and L; *OXALIDACEAE*, G and I

A, *Geranium robertianum* Linn. Stem $\times 15$. B, *Impatiens glandulifera* Royle. Petiole $\times 10$. C, *Geranium pyrenaicum* Burm. f. Petiole $\times 12$. D, *Erodium moschatum* (L.) Hér. Stem $\times 7$. E, *Tropaeolum majus* Linn. Petiole $\times 7$. F, *Pelargonium zonale* (L.) Ait. Petiole $\times 12$. G, *Oxalis corniculata* Linn. cult. var. Stem $\times 15$. H, *Impatiens glandulifera* Royle. Stem $\times 10$. I, *Oxalis corniculata* Linn. Petiole $\times 15$. J, *Pelargonium zonale* (L.) Ait. Stem $\times 7$. K, *Geranium pyrenaicum* Burm. f. Stem $\times 7$. L, *Tropaeolum majus* Linn. Stem $\times 7$.

e. Endodermis. hp. Hollow pith. pp. Parenchymatous pith.

ECONOMIC USES

Geranium oil is distilled chiefly from the leaves of selected varieties of *Pelargonium*. Many species of *Geranium* and *Pelargonium* are cultivated for ornamental purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Biebersteinia, Erodium,* Geranium,* Monsonia, Pelargonium,* Sarcocaulon, Viviania, Wendtia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Balbisia), (Geranium), (Monsonia), (Pelargonium), (Viviana), (Wendtia).

LITERATURE

(i) On General Anatomy

Doyle 609, Evenari (Schwarz) 665, Holm 1026, Knuth 1251, 1252, 1255, Legault 1342, Planchon 1728, Sabnis 1977, Scott and Whitworth 2074, Thompson 2254, Zemke 2505.

(ii) On Wood Structure

Barghoorn 139, Heimsch 938, Macduffie 1408, Record 1843, 1851, Thompson, W. P. 2254.

X 75. BALSAMINACEAE

(FIG. 70 on p. 296)

SUMMARY

A small family of succulent herbs belonging to the genera *Impatiens* and *Hydrocera*. The family is mainly tropical but some species occur in temperate regions. The most characteristic anatomical feature is the occurrence of **raphides**.

LEAF

Dorsiventral. **Extra-floral nectaries** recorded on the petiole and stem of certain species of *Impatiens*. **Hydathodes** present in the leaf teeth. **Stomata** confined to the lower surface in *I. sultani* Hook. f., but observed on both surfaces in other species of *Impatiens* examined at Kew; mostly ranunculaceous but some tending to be cruciferous. **Petiole** in transverse sections through the distal end of *Impatiens glandulifera* Royle (Fig. 70 B) exhibiting an arc of separate bundles, but with thin-walled tissue, resembling phloem, present between the phloem groups of the individual bundles. **Raphide-sacs** present in the leaf (and stem) of at least 62 species of *Impatiens*, sometimes appearing as transparent dots; frequently containing mucilage as well as raphides. Branched **tannin-sacs** present in the spongy parenchyma of *I. sultani*.

AXIS

STEM (Fig. 70 H)

Epidermis composed of small, thin-walled cells. **Cortex** relatively narrow, outer part consisting of small collenchymatous cells and the inner part of

large, thin-walled cells in the few species examined. **Pericycle** apparently devoid of sclerenchyma, the rigidity of the stem being maintained by the strongly turgescient ground tissue. **Vascular bundles** individually distinct and arranged in a circle of about 12 as seen in transverse sections; consisting mainly of xylem composed of a ground tissue of small, very thin-walled cells with large vessels embedded in it, the latter being provided with very well-developed spiral thickening. Phloem strands in each bundle small, those of adjacent bundles being connected together by a small-celled tissue with thin walls, rather suggesting phloem in appearance, the true nature of which needs further investigation. Vessels with simple perforations. **Interfascicular cambium** arising, in older stems, in the region of the small-celled tissue just mentioned, but apparently giving rise only to thin-walled tissue on the inside, comparable with the ground tissue of the xylem, but not including any vessels. **Pith** becoming hollow at the centre. Isolated, annular, or spiral vessels stated by Solereder to arise in the pith of certain species of *Impatiens* before the development of the vascular bundles. Large cells with mucilaginous contents scattered throughout the ground parenchyma. Bundles of **raphides** present in the cortex.

TAXONOMIC NOTES

Impatiens was included by Bentham and Hooker in the Geraniaceae, from which the genus differs, however, (i) in having an arc instead of a circle of bundles in the petiole, (ii) in the absence of a ring of mechanical tissue from the pericycle, (iii) in the presence of raphide sacs. These anatomical features confirm the desirability of treating the Balsaminaceae as a separate family.

ECONOMIC USES

Several species of *Impatiens* are cultivated for ornamental purposes.

GENUS DESCRIBED

Impatiens.* The description of the petiole and stem structure is based mainly on an examination of *I. glandulifera* Royle grown at Kew.

* Represented in the Kew slide collection.

76. LIMNANTHACEAE

SUMMARY

A small family of succulent marsh herbs occurring in North America. The anatomy has been studied especially by Russell (1969) on whose paper the following description is mainly based.

LEAF

Dorsiventral. **Epidermis** consisting of rounded, unthickened cells. **Stomata** present on both surfaces, but more numerous on the lower than on the upper side. **Mesophyll** consisting of 1 layer of palisade tissue interrupted by intercellular spaces below the stomata, and a narrow zone of spongy tissue below the palisade with small bundles embedded in it. A single **hydathode**

is present at the tip of the leaf. **Tannin cells** occur on the lower side of the leaf in *Limnanthes*, but not seen in *Floerkea*.

AXIS

STEM

Weak and flaccid, remaining green and rarely branched in *Floerkea*; stouter and more branched, especially at the base, in *Limnanthes*. **Epidermis** composed of small rectangular slightly cutinized cells. **Cortex** 6–7 layered, consisting of large round cells with thin walls. **Endodermis** indistinct. **Vascular bundles** 8–10 in a ring, appearing individually distinct and separate in transverse sections. Phloem poorly developed. Interfascicular cambium absent.

ROOT

Root system consisting of a few short, fibrous, unbranched roots. Adventitious roots also arise from the nodes in procumbent species. **Epidermis** cutinized in mature roots. **Cortex** consisting of 2–4 layers of large round cells with thin walls. **Endodermis** well defined, consisting of elliptical cells thickened on the inner tangential and lateral walls. **Stele** consisting of a simple diarch bundle.

TAXONOMIC NOTES

Limnanthes was included in the Geraniaceae in the system of Bentham and Hooker, but more recently this and the anatomically similar genus *Floerkea* have been placed in a separate family the Limnanthaceae. The anatomical characters in themselves scarcely provide sufficient evidence to determine whether they should constitute a separate family or not. It is interesting to note, however, that the Limnanthaceae resembles the Geraniaceae in having widely spaced vascular bundles in the stem, but there is, on the other hand, no trace of the characteristic mechanical ring in the pericycle.

GENERA EXAMINED

Floerkea, *Limnanthes*.

LITERATURE

On General Anatomy
Russell 1969.

✓77. OXALIDACEAE

(FIG. 69 on p. 290; FIG. 70 on p. 296; FIG. 77 on p. 334)

SUMMARY

(i) GENERAL

Most members of the family are herbs, but a few shrubby species occur, whilst a still smaller number resemble small trees. They mostly occur in tropical and sub-tropical regions, but some species are temperate. There is a great diversity of form even amongst the herbaceous species, since some are rosette plants with no true stem, others have an underground rhizome, whilst

there are fleshy and woody species which serve as transitions to the shrubby and arboreal types. Members of the *tuberosae* section of *Oxalis* bear small root tubers, whilst in other sections of the genus there are species with contractile roots or bulbs. Other interesting features include the conversion of petioles into phyllodes after abscission of the leaflets in certain species of *Oxalis*, and the possession of leaves which exhibit 'sensitive' movements. In correlation with the range of habit there is a correspondingly wide diversity of anatomical features. The fundamental **vascular structure** of both stem and petiole consists of a circle of collateral bundles, often accompanied externally by a sclerenchymatous ring in the **pericycle**. In some species of *Oxalis* the xylem of the stem tends to be in the form of a closed cylinder in correlation with a more woody habit, but this character has been developed even further in genera like *Averrhoa*, where the xylem and phloem of the petiole as well as of the stem appear, in transverse sections, as practically continuous closed rings. **Secretory cavities** are characteristic of many species of *Oxalis* where they occur in the leaf. As the name of the family implies, oxalic acid is very common in the tissues, where it is believed to occur in the form of dissolved potassium oxalate as well as being secreted as calcium oxalate, usually in the form of small, solitary, cubical crystals. Crystal-sand is said to occur as well but only very rarely.

(ii) Wood

Vessels often in multiples of 4 or more cells, perforations simple, intervascular pitting alternate and large, pits to parenchyma often simple, members of medium length to very short. **Parenchyma** typically vasicentric and scanty, but often with numerous diffuse crystalliferous strands. **Rays** uniseriate, heterogeneous to almost homogeneous. **Fibres** septate, with simple pits, moderately to very short.

LEAF

Leaflets usually dorsiventral in *Oxalis*. Simple, unbranched, **hairs** of variable length widely distributed in the family. Bladder-like hairs which serve for water storage recorded in species of *Oxalis*. Glandular hairs, with stalks of varying lengths and unicellular heads, stated to occur in *Averrhoa*, *Biophytum*, and *Oxalis*. Cells of the **epidermis** of *Oxalis* often very large in proportion to the total width of the lamina, sometimes arched outwards; in some species tall, palisade-like, exceeding the remainder of the total thickness of the leaf. Lower epidermis papillose in certain species of *Eichleria* and *Oxalis*. **Stomata** rubiaceous with at least 1 and sometimes 2 subsidiary cells parallel to the pore in *Averrhoa*, *Biophytum*, and *Eichleria*. **Hydathodes** in depressions in the leaflets of certain species of *Oxalis* described by Vouk (2342). **Hypoderm** present in *Dapania scandens* Stapf. Vascular bundles of the **veins** provided with enlarged terminal tracheids in *Averrhoa*, *Biophytum*, and *Eichleria*. **Petiole**, in transverse sections, exhibiting a circle of separate bundles in many species of *Oxalis*. The phloem groups of the bundles in the petiole are attached externally to a ring of sclerenchyma in some species, e.g. *O. corniculata* Linn. (Fig. 70 1), but not in others, e.g. *O. rosea* Jacq. Closed rings of xylem and phloem surrounding 2 medullary bundles recorded by Solereder in the distal end of the petiole of *Oxalis tetraphylla* Cav. The

xylem and phloem form a practically continuous cylinder around a fairly extensive, thin-walled, parenchymatous pith in *Averrhoa carambola* Linn. (Fig. 77 c). The vascular cylinder is also surrounded by a relatively broad, almost continuous ring of thick-walled fibres in the same species. **Secretory cavities**, variously interpreted as being schizogenous or lysigenous in origin, containing either brown or red, and sometimes transparent and crystalline substances, present in the pinnules of *Oxalis* spp., from both South Africa and America. These cavities, which occur in different positions in the various species, are confined to the margins of the pinnules in some, but cover the whole surface in others, e.g. *O. articulata* Sav. and *O. hirta* Linn. Secretory cavities absent from certain species of *Oxalis* with a well-developed stem, e.g. *O. cernua* Thunb. and *O. deppei* Lodd.; generally situated on the dorsal side of the vascular bundles when occurring on the bulb scales; often elongated and resembling canals. The distribution of secretory cavities and canals may be of specific diagnostic value, but further investigation is necessary in order to determine this point. **Crystals** mostly solitary, sometimes appearing as transparent dots in certain species of *Oxalis*. Crystal cells also accompany and form sheaths to the vascular bundles of the veins in *Averrhoa*, *Biophytum*, and *Eichleria*.

In certain species of *Oxalis* the leaflets become detached from the petiole, which then constitutes a phyllode. This is well seen, for instance, in *O. herrerae* R. Knuth and *O. bupleurifolia* St. Hil., as described by Metcalfe (1495). In the first of these species, the petiole becomes considerably swollen and club-shaped after the leaflets have fallen, as they usually do when the plant is growing in an exposed position. The increase in the bulk of the petiole is caused by enlargement of the parenchymatous tissues of which the petiole is mainly composed. The chlorophyll-containing tissue immediately below the epidermis becomes more palisade-like; the epidermal cells become larger, the cuticle thicker, and the stomata more numerous. There is a circle of small, individually distinct bundles in both swollen and unswollen petioles. In *O. bupleurifolia* the petiole is flattened and leaf-like; stomata are present on both surfaces. The ground tissue of the petiole consists of loosely arranged parenchymatous cells containing chloroplasts. Vascular bundles interspersed with fibre bundles are present towards the abaxial side. The bundles on the adaxial side consist exclusively of fibres and probably represent reduced fibro-vascular strands in a petiole which was originally radially symmetrical.

Leaves of certain members of the family exhibit 'sensitive' movements comparable with those which are more familiar in certain members of the Leguminosae. According to Steckbeck (2190) sensitive movements can be especially well observed in *Biophytum sensitivum* DC. and *B. dendroides* DC.

AXIS

STEM (Fig. 70 G and 77 K)

Epidermis consisting of cells of rather variable sizes in the few species of *Oxalis* examined. **Cork** well developed in *Averrhoa*, *Connaropsis*, *Eichleria*. **Cortex** relatively narrow, composed of large, loosely packed parenchymatous cells in *Oxalis* and of cells containing oil and large solitary crystals in *Averrhoa carambola* Linn. **Pericycle** bounded by a composite and more or less continuous ring of sclerenchyma in *Averrhoa*, *Biophytum*, *Connaropsis*,

Dapania, *Eichleria*, *Hypseocharis*, and *Oxalis* (pro parte). **Vascular bundles** collateral, widely separated, arranged in a single ring in *Oxalis corniculata* Linn. (Fig. 70 G) and *O. rosea* Jacq. Bundles individually distinct, arranged in a single ring in young stems of *Oxalis herrerae* R. Knuth but with a closed cylinder of xylem in older stems of the same species. Phloem and xylem constituting closed rings in *Averrhoa carambola* Linn. (Fig. 77 K). Vessels small (radial diameter seldom exceeding $40\ \mu$ in *Averrhoa carambola* Linn. or $30\ \mu$ in *Oxalis corniculata* Linn.), solitary or in short radial rows; perforations simple. Ground tissue of the xylem consisting of moderately thick-walled prosenchymatous elements in *Averrhoa carambola*, locally replaced by cells each of which contains a row of solitary crystals. **Pith** consisting of large, thin-walled parenchyma in *Oxalis corniculata* and *O. rosea* Jacq.; some of the cells with oily contents in *Averrhoa carambola*. Pith stated to contain fibres in *Dapania scandens* Stapf.

WOOD (Fig. 69 A-C)

Vessels medium-sized ($100\text{--}200\ \mu$ mean tangential diameter) or slightly less; solitary, in multiples that often exceed 4 cells, and sometimes in irregular clusters; about 5 per sq. mm.; sometimes with faint spiral thickening in *Sarcotheca*. Perforations simple. Intervascular pitting alternate, large; pits to ray and wood parenchyma commonly simple and sometimes larger than the intervacular pitting, but tending to be round rather than elongated; occasionally unilaterally compound. Mean length $0.3\text{--}0.7$ mm. **Parenchyma** consisting of a few cells about the vessels, with, in most species, numerous crystalliferous strands scattered among the fibres (Fig. 69 B). The strands of vasicentric parenchyma of 4-12 cells, the crystalliferous strands with 25-45 chambers. **Rays** typically exclusively uniseriate, but most species with a few biseriate rays, particularly in *Connaropsis griffithii* Planch.; 10-20 per mm.; distinctly heterogeneous with 1 or 2 marginal rows of rather high upright cells, e.g. in *Averrhoa carambola* Linn. to almost homogeneous in *Sarcotheca subtriplineris* Hall. f. Containing crystals in some species of *Averrhoa*. Heimsch (938) notes that the rays are very poorly developed in some species of *Oxalis*. **Fibres** with numerous small, simple pits on the radial walls; probably all septate in *Averrhoa* and *Sarcotheca*, but with septate fibres tending to be limited to the neighbourhood of the vessels in *Connaropsis griffithii*. Walls thin to thick. Mean length $0.5\text{--}1.0$ mm.

RHIZOME

Cork very thick, and wood very well developed in *Hypseocharis* according to Chauvel (380).

ROOT

Certain species of *Oxalis* are provided with contractile roots bounded externally by a few layers of **cork**, the bulk of the root being composed of **secondary phloem**, consisting of radial rows of parenchymatous cells with isolated sieve tubes scattered throughout. **Cortex** narrow, parenchymatous. **Stele** tetrarch when young. The root is cast off from the plant by an abscission layer after having fulfilled its function. According to Duncan (614) and

Rohde (1946) the contraction which serves to pull the plant into the ground is achieved by the secondary phloem. The cells are vertically elongated at first and filled with sap of high osmotic value. The osmotic value of the sap is subsequently reduced by chemical changes which are accompanied by the formation of insoluble substances such as calcium oxalate. The cells then contract longitudinally and, as the plant is securely anchored by the base of the root, it tends to be pulled into the ground.

TAXONOMIC NOTES

The Oxalidaceae were included in the Geraniaceae in the system of Bentham and Hooker. There are certain anatomical features common to both of these families which confirm that they may be closely related to one another. The basic vascular structure of the stem and petiole in both of them consists of a ring of separate collateral bundles frequently associated with a characteristic and well-developed sclerenchymatous ring in the pericyclic region. There are aberrations from this type in both families, especially in species which tend to be shrubby or arborescent in habit, where the xylem of adjacent bundles becomes connected so as to form a continuous ring as the plant grows older.

Heimsch (938) concludes that the wood anatomy justifies the placing of *Sarcotheca* in this family rather than in the Linaceae.

ECONOMIC USES

The tubers of certain species of *Oxalis* are edible. The fruits of the Bilimbi (*Averrhoa bilimbi* Linn.) and the Carambola (*A. carambola* Linn.) are preserved and eaten in India. Oxalic acid is especially abundant in *Oxalis* spp. and can be extracted.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Averrhoa,* *Biophytum*, *Connaropsis*, *Dapania*, *Eichleria*, *Hypseocharis*, *Oxalis*.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Averrhoa, *Connaropsis*, (*Oxalis*), *Sarcotheca*.

LITERATURE

(i) *On General Anatomy*

Chauvel 380, Duncan 614, Knuth 1253, 1254, Metcalfe 1495, Rohde 1946, Steckbeck 2190, Vouk 2342.

(ii) *On Wood Structure*

Heimsch 938, Janssonius 1154, Kanehira 1206, Lecomte 1334, Record 1851.

78. TROPAEOLACEAE

(FIG. 70 on p. 296)

SUMMARY

Succulent, often scandent herbs from the Andes and other parts of Central and South America. Some species are characterized by tuberous roots. Owing to the small number of species which have been studied, the characters are described under the organs in which they occur.

LEAF

Hairs infrequent, unbranched, consisting of several cells. Hill (969) induced the formation of unicellular hairs on the usually glabrous petioles of *T. aduncum* Smith by surgical manipulations such as removing the lamina. **Epidermis** containing cells with mucilaginous contents in *Tropaeolum majus* Linn. **Stomata** always present on the lower surface and in many species on the upper side as well; ranunculaceous. **Water pores** terminate the vascular bundles in *T. majus*. Drops of liquid exuded from the leaf veins, petiole, and young stem of *T. majus* when cut, are stated by Solereder to arise from persistently juvenile vessel elements with nucleus and protoplasmic contents. **Petiole** (Fig. 70 E) in transverse sections through the distal end of the few species examined, exhibiting a single ring of separate, collateral bundles embedded in thin-walled parenchyma; mechanical tissue absent. Spherical **secretory cells**, with highly refractive contents, appearing as dots when examined with a lens, recorded in *T. pentaphyllum* Lam.; sphaero-crystalline masses of the same substance said to occur in *T. majus* var. **Myrosin** present but not apparently localized in special cells (cf. stem and root).

AXIS

STEM (Fig. 70 L)

Epidermis consisting of comparatively small cells. **Cork** stated to arise in the endodermis of *T. peregrinum* Linn.; but apparently more superficial in species examined at Kew. **Cortex** narrow, consisting of thin-walled parenchyma. **Endodermis** fairly well defined and provided with casparian thickenings in *T. majus* Linn. **Vascular bundles** (Fig. 70 L), at first separate, somewhat variable in size, arranged in a single ring; the xylem groups of the originally separate bundles later become connected by prosenchymatous elements with simple pits, formed on the inside of an interfascicular cambium. Interfascicular phloem is also formed by the activity of the cambium. Vessels of *T. aduncum* Smith and *T. majus* up to about 80 μ in radial diameter occupying the greater part of the transverse area of each of the bundles; those first formed are provided with spiral thickening, but the later ones possess small bordered pits; perforations usually simple, but reticulate types and transitional forms have also been recorded by Thompson (2254). **Pith** occupying the greater part of the stem, composed of thin-walled, somewhat loosely arranged parenchyma. **Myrosin cells**, capable of detection with Millon's reagent, present in the sub-epidermal region as well as in the phloem. Contrary to Solereder's statement, no mechanical tissue was observed in the pericycle.

Root

Myrosin cells present in the primary cortex and phloem. The statement that septate laticiferous tubes occur in the tuberous roots of a few species requires confirmation.

TAXONOMIC NOTES

The genus *Tropaeolum* was included in the system of Bentham and Hooker in the Geraniaceae, but since then it has generally been treated as a separate family related to the Geraniaceae. The arrangement of the vascular bundles in the stem and petiole is similar to that of the Geraniaceae, but the very well-developed ring of mechanical tissue in the pericycle, which is a very characteristic feature of the Geraniaceae, does not exist in the species of *Tropaeolum* available for examination. Myrosin, which is commonly present in *Tropaeolum*, has not apparently been found in the true Geraniaceae. These facts favour the inclusion of *Tropaeolum* in a distinct family, which may, however, have affinities with the Geraniaceae, although the anatomical features are not very conclusive concerning this relationship. It is interesting to note that myrosin also occurs in the Cruciferae, Resedaceae, and Cappariaceae, which are not generally regarded as close relatives of the Tropaeolaceae.

ECONOMIC USES

Several species of *Tropaeolum* are commonly cultivated in gardens for ornamental purposes, the best-known example being the Nasturtium.

GENUS DESCRIBED

Tropaeolum.* Except where otherwise stated, the above description is based on an examination of *T. aduncum* Smith and *T. majus* Linn. grown at Kew.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Farenholtz 671, Hill 969, Thompson 2254.

✓ 79. RUTACEAE

(FIG. 71 on p. 306; FIG. 72 on p. 306; FIG. 73 on p. 312; FIG. 77 on p. 334; FIG. 80 on p. 350)

SUMMARY

(i) GENERAL ANATOMY

A family consisting mainly of trees or shrubs and a very small proportion of herbs all of which flourish in the tropics and sub-tropics. There is a considerable range in the shape of the leaves in different sections of the family, whilst thorns are common in some of the genera. The ground tissue of both leaf and axis is nearly always characterized by the presence of **secretory cavities** which, in the leaf, appear to the naked eye as transparent dots. The secretory cavities are sometimes replaced or accompanied by **secretory cells**. **Resin cells** are common in the pith, primary cortex, and rays of the young

stem. The **hairs** are predominantly thick-walled and unicellular or sometimes uniseriate, but peltate, tufted, stellate, and multicellular glandular hairs or warts also occur. The **epidermis** of the leaf is frequently composed of

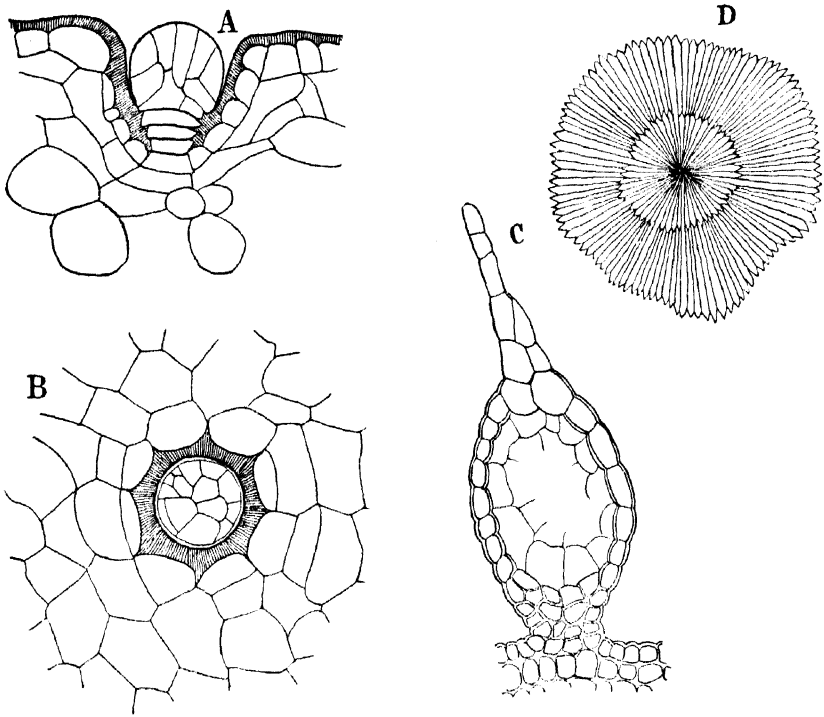


FIG. 71. RUTACEAE

A-B, Glandular hair from the leaf of *Toddalia aculeata* Pers., A in section, B in surface-view. C, Glandular shaggy hair from the floral region of *Dictamnus albus* Linn. D, Peltate hair of *Phebalium anceps* DC.—A-B by Solereder, C after Rauter, D after O. Bachmann.

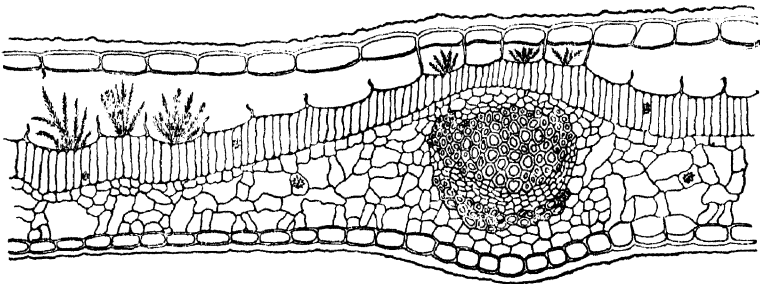


FIG. 72

Transverse section through the leaf of *Barosma serratifolia* (Curt.) Willd.—By Solereder.

cells of which the inner walls are mucilaginous. **Stomata** are of various types. The usually abundant **crystals** of calcium oxalate may be either solitary or clustered, or a mixture of both of these types. Raphides and crystal-sand also occur, although more infrequently. Dendritic crystals of diosmin have been

recorded in a number of genera; berberin has been detected by Klein and Bartosch (1245) in certain species of *Evodia*, *Orixa*, *Toddalia*. There is usually a solitary, arc-shaped or cylindrical vascular strand in transverse sections through the distal end of the **petiole** in most of the species which have been examined. A notable exception is *Ruta graveolens* Linn. with an arc of separate bundles. **Cork** arises superficially in the stem of all of the species in which its development has been studied, and in some species consists of thin-walled cells, but in others the outer tangential walls are strongly thickened. The **pericycle** of the stem usually contains well-defined strands of fibres, although there is a tendency for the groups to coalesce in certain species. The **xylem** and **phloem** constitute a closed cylinder in the stem in nearly all species, although the primary medullary rays are moderately broad in a few instances.

(ii) WOOD

Vessels small to medium-sized, often very small, typically in multiples and sometimes with a distinct radial or oblique pattern, ring-porous or semi-ring-porous in some species; perforations exclusively simple except for rare multiperforate plates in a few species; intervacular pitting alternate, small to minute, pits to rays cells similar; members usually of medium length, sometimes moderately to very short. **Parenchyma** (a) terminal, (b) paratracheal, usually vasicentric, but aliform and confluent in some genera, and (c) diffuse, in some genera only, and often consisting largely of chambered crystal cells. **Rays** exclusively uniseriate or up to 2-4 cells wide; considerably larger in a few genera; homogeneous or weakly heterogeneous and with few uniseriate rays in most genera, but sometimes distinctly heterogeneous and with numerous uniseriate rays; with distinct stories only in *Chloroxylon*, but in echelon in a few other genera. **Fibres** with simple or slightly bordered pits, with occasional septa in a few species; of medium length to moderately short. **Tracheids** rare. Normal **intercellular canals** absent, but traumatic vertical canals moderately common.

LEAF

Generally dorsiventral but sometimes centric. **Hairs** infrequent in many members of the family, but both clothing and secretory types occur. Clothing hairs most frequently thick-walled, unicellular; tufted types recorded in *Boronia*, stellate forms in species of *Asterolasia*, *Chorilaena*, *Correa*, *Crowea*, *Diplolaena*, *Eriostemon*, *Flindersia* (Fig. 80 B), *Phebalium*, *Zieria*, and scales in *Eriostemon*, *Flindersia*, *Nematolepis*, *Phebalium* (Fig. 71 D). Adpressed hairs, unicellular when young, but becoming septate and deciduous with increase in age, recorded by Swingle (2225) in the drought resistant *Eremocitrus glauca* Swingle (the Desert Kumquat) from Australia. External glands with clavate or spherical multicellular heads recorded in certain species of *Choisya*, *Dictyoloma*, *Esenbeckia*, *Monnieria*, *Pilocarpus*, *Toddalia* (Fig. 71 A-B), *Zanthoxylum*, and *Zieria*. Sessile glands also occur on the lower surface of the leaf in *Boronia*. Glandular shaggy hairs recorded in the floral region in *Dictamnus albus* Linn. (Fig. 71 C). **Cork warts** sometimes present on the surface of old *Citrus* leaves. Cells of the **epidermis** frequently have mucilaginous inner walls in *Acmadenia*, *Adenandra*, *Agathosma*, *Barosma*, *Coleonema*, *Diosma*,

Empleurum, *Flindersia*, *Macrostylis*, *Phellodendron*, *Skimmia*, *Toddalia*, *Zanthoxylum*. Epidermis papillose in species of *Boenninghausenia*, *Dictyoloma*, *Eriostemon*, *Pilocarpus*, and *Spiranthera*. Upper epidermis containing groups of small cells with the palisade especially well developed below them in *Murraya exotica* Linn. **Stomata** sometimes present on both surfaces (*Cneoridium dumosum* Hook. f. and *Ruta graveolens* Linn.), but generally confined to the lower side in most species; limited to a narrow median zone in *Acmadenia* and *Coleonema*, and to two narrow strips on the lower surface situated on either side of the midrib in *Macrostylis*; protected by scales in *Phebalium filifolium* Turcz. Stomata provided with variously arranged subsidiary cells in different genera and species.

Studies by Hirano (1979) and Reed (1897) of the distribution of the stomata on the leaves of a number of species of *Citrus*, collected and cultivated in one place, showed the density to be related to the country of origin. Most tropical species were found to have more than 500 stomata per sq. mm., but in the hardier species and varieties from outside the tropics, with but few exceptions, the density was lower. Stomatal density was also found to vary within the single species *Citrus sinensis* Osbeck according to the stage of development of the leaf, being greatest in very young leaves at the end of a period of stomatal initiation. The size of the stomata was found to be only slightly influenced by the number per unit area, but reduction of the light intensity decreased their density. McLean (1468) found the greater resistance of the Szinkum Mandarin (*Citrus aurantium* Linn. var. *szinkum*) to the canker induced by infection with *Pseudomonas citri* Hasse compared with the lower resistance of the Florida Grape-fruit (*C. grandis* Hassk.) to be associated with differences in the structure of the openings to the outer chamber to the stomata; those of the more resistant of these species being made narrower by the development of larger ridges. The structure of *Citrus* stomata has also been investigated by Turrell (2301). One or more layers of **hypoderm**, sometimes locally distributed, occur in species of *Cusparia*, *Eriostemon*, *Evodia*, *Pagetia*, *Pilocarpus*, *Ruta*. **Mesophyll** in the adpressed leaves of *Agathosma lediformis* E. et Z. described by Solereder as having the palisade tissue more strongly developed on the lower than on the upper side; isobilateral in *Eremocitrus glauca* Swingle, the Australian Kumquat according to Swingle (2225) and in *Geijera parviflora* Lindl. according to Wood (2457). Branched sclerenchymatous cells are associated with the terminations of the veins in several species of *Boronia*. **Petiole**, in transverse sections, usually exhibiting a closed cylinder of xylem and phloem at the distal end, notably in species of *Calodendrum*, *Casimiroa*, *Choisya* (slightly interrupted in *C. ternata* H. B. and K. (Fig. 77 G)), *Citrus*, *Correa*, *Dictamnus*, *Evodia*, *Murraya*, *Phellodendron*, *Pilocarpus*, *Ptelea*, *Ravenia*, *Toddalia*, *Zanthoxylum*; with a closed cylindrical bundle accompanied by medullary ones in *Galipea*; with a solitary arc-shaped strand in species of *Adenandra*, *Barosma* (Fig. 77 E), *Boronia*, *Orixa* (phloem present on part of the dorsal as well as on the ventral side of each strand), *Skimmia*; with an arc of separate bundles in *Ruta graveolens* Linn. (Fig. 77 B). Vascular strand of the petiole usually accompanied by a circle or groups of pericyclic fibres except sometimes in species of *Boronia*, *Calodendrum*, *Correa*, *Orixa*, *Ptelea*, *Skimmia*. **Secretory cavities** appearing as transparent dots either in the uninjured leaf or on a cut surface, and variously interpreted as

schizogenous or lysigenous, almost always present in the mesophyll. **Resin cells** have been recorded in *Cneoridium*. Tanniniferous idioblasts are stated by Wood (2457) to occur in the mesophyll of *Geijera parviflora* Lindl. **Crystals** very common, solitary ones being especially characteristic of certain genera and clustered ones more frequent in others. Some of the palisade cells transversely septate and containing clustered crystals in *Pilocarpus* spp. Raphides and/or styloids recorded in *Erythrochiton*, *Monnieria*, *Raputia*, and *Rauia*; crystal-sand in *Cusparia* and *Orixa*. **Hesperidin** (diosmin), usually in the form of dendritic crystals, soluble in and giving a yellow colour to solutions of caustic potash, recorded in the epidermis of certain species of *Agathosma*, *Barosma* (Fig. 72), *Calodendrum*, *Dictamnus*, *Empleurum*, *Pilocarpus*, *Ptelea*, *Skimmia*, *Toddalia*, *Zanthoxylum*.

AXIS

YOUNG STEM (Fig. 77 H)

Hairs of the following kinds have been recorded or observed. (i) Unicellular, thick-walled in species of *Agathosma*, *Calodendrum*, *Choisya*, *Dictamnus*, *Evodia*, *Melicope*, *Murraya*, *Orixa*, *Ptelea*, *Ravenia*, *Skimmia*, *Zanthoxylum*. (ii) Uniseriate in species of *Casimiroa* and *Evodia*. (iii) Stellate in species of *Calodendrum* and *Correa* spp. (iv) Glandular, club-shaped in *Agathosma* and *Evodia*. **Cork** arising in the sub-epidermis in those species so far investigated, notably in species of *Agathosma*, *Barosma*, *Calodendrum*, *Casimiroa*, *Citrus*, *Evodia*, *Melicope*, *Murraya*, *Orixa*, *Phellodendron*, *Ptelea*, *Ruta*, *Skimmia*, *Zanthoxylum*. Cork cells thin-walled in species of *Casimiroa*, *Cusparia*, *Galipea*, *Murraya*, *Ravenia*, *Ruta*. Outer tangential walls of cork cells strongly thickened in *Agathosma*, *Barosma*, *Orixa*, *Ptelea*, *Skimmia*, and *Zanthoxylum*. Primary **cortex** containing stone cells in certain species of *Almeidea*, *Casimiroa*, *Cusparia*, *Metrodorea*, *Ptelea*, and *Ravenia*. **Cortical bundles** sometimes present in *Eriostemon* and *Pilocarpus*. **Pericycle** usually containing isolated strands or bands of sclerenchyma, notably in certain species of *Adenandra*, *Agathosma* (groups small), *Barosma* (small and inconspicuous), *Boronia*, *Casimiroa* (very small), *Citrus*, *Correa* (not very widely separated), *Dictamnus*, *Eriostemon* (very poorly developed), *Evodia*, *Melicope*, *Murraya* (in older stems), *Phellodendron*, *Pilocarpus* (associated with large stone cells), *Poncirus*, *Ptelea* (not well developed), *Ruta* (small), *Toddalia*, *Zanthoxylum*. Pericyclic sclerenchyma less frequently tending to constitute a continuous ring, but this character is sometimes to be seen in *Amyris*, *Calodendrum*, *Choisya*, *Correa*, *Evodia*, *Murraya*, *Orixa*, *Paramignya*, *Zanthoxylum*. Pericyclic fibres apparently absent from certain species of *Boeninghausenia*, *Coleonema*, *Crowea*, *Euchaetia*, *Ptelea*, *Ravenia*, and *Skimmia*. **Phloem** and **xylem** constituting closed cylinders traversed by narrow rays in all of the species examined except in *Choisya*, *Eriostemon*, and *Pilocarpus*, where relatively broad primary rays sometimes occur, especially in very young stems. Vessels arranged in well-defined radial rows in certain species of *Adenandra*, *Agathosma*, *Barosma*; *Boronia* (thin-walled), *Calodendrum*, *Dictamnus*, *Melicope*, *Murraya*, *Ravenia*, but with the radial arrangement less pronounced in species of *Citrus*, *Crowea*, *Eriostemon*, *Orixa*, *Ruta*, *Zanthoxylum*. Vessels not in well-defined radial rows in some species of *Casimiroa*, *Choisya*, *Citrus*, *Evodia*, *Phellodendron*, *Ptelea*, *Skimmia* (flame-

shaped arrangement of small vessels), *Toddalia* (mostly solitary). Vessels usually with simple perforations. **Pith** homogeneous in species of *Agathosma*, *Barosma*, *Boronia*, *Calodendrum*, *Casimiroa*, *Choisya*, *Correa*, *Crowea*, *Dictamnus*, *Eriostemon*, *Orixa*, *Phellodendron*, *Ptelea*, *Ruta*, *Skimmia*, *Zanthoxylum*; heterogeneous in species of *Citrus*, *Evodia*, *Melicope*, *Murraya*, *Pilocarpus*, *Toddalia*. **Medullary cork** recorded by Holm (999) in the hypocotyl of seedlings of *Balsamocitrus dawei* Stapf, but not in other closely related genera. Large conspicuous **secretory cavities**, usually with oily or resinous contents, very common in the parenchymatous tissues, especially the cortex, notably in species of *Adenandra*, *Agathosma*, *Barosma*, *Calodendrum*, *Casimiroa*, *Choisya*, *Citrus*, *Dictamnus* (relatively infrequent), *Eriostemon* (specially large), *Melicope*, *Murraya*, *Orixa*, *Phellodendron* (sometimes infrequent), *Pilocarpus*, *Poncirus*, *Ptelea* (sometimes specially large), *Ravenia*, *Ruta*, *Skimmia*, *Toddalia*, *Zanthoxylum* (sometimes infrequent). Secretory cavities sometimes partly or wholly replaced by **secretory cells** in certain species of *Boronia*, *Citrus*, *Correa*, *Crowea*, *Melicope*, *Phellodendron*, *Ravenia* (contents deeply stained with safranin), *Toddalia*, *Zanthoxylum* (situated in the inner part of the cortex or in the phloem). Intercellular secretory spaces present in *Evodia* and secretory canals in *Clausena* sp. **Crystals** commonly abundant in the cortex and/or pith and sometimes in the phloem as well, e.g. in species of *Adenandra*, *Agathosma*, *Barosma*, *Calodendrum*, *Casimiroa*, *Choisya*, *Citrus*, *Eriostemon*, *Murraya*, *Pilocarpus*, *Poncirus*, *Ptelea*, *Ravenia*, *Ruta*, *Skimmia*, *Toddalia*, *Zanthoxylum*. Crystals predominantly solitary in species of *Casimiroa*, *Citrus*, *Murraya*, *Pilocarpus*, *Poncirus*, *Ravenia* (very large), *Toddalia*; usually clustered in certain species of *Adenandra*, *Agathosma*, *Barosma*, *Calodendrum*, *Choisya*, *Eriostemon*, *Pilocarpus*, *Ptelea*, *Ruta*, *Skimmia*. Raphides and/or styloids present in certain species of *Erythrochiton*, *Galipea*, *Monnieria*, *Raputia*, *Ravenia*, and *Rauia*, and sacs of crystal-sand in *Cusparia* sp. and *Orixa* sp. Dendritic crystals of diosmin recorded in *Barosma*, *Eriostemon*, *Skimmia*, *Toddalia*.

WOOD (Fig. 73)

Vessels mostly very to moderately small (25–100 μ mean tangential diameter), sometimes extremely small (less than 25 μ), e.g. in *Choisya* and *Skimmia*, medium-sized in about one-third of the genera and never more than 200 μ in mean diameter (excluding ring-porous species); never exclusively solitary, radial multiples of 2–4, or more, common, the pores retaining a characteristic rounded shape; clusters moderately common in *Aeglopsis*, *Balsamocitrus*, *Bosistoa*, *Erythrochiton*, *Feronia*, *Glycosmis*, *Halfordia*, *Limonia*, *Nycticalanthus*, *Oricia*, *Phebalium*, *Ptelea*, *Skimmia*, and *Zieria*; multiples and clusters sometimes forming a radial or oblique pattern, most marked in *Acradenia*, *Acronychia* p.p., *Amyris* (Fig. 73 L), *Balfourodendron*, *Calodendrum*, *Choisya*, *Cneoridium* (938), *Evodia* p.p., *Orixa* (938), *Phebalium*, *Ptelea*, *Raputia*, *Skimmia*, and *Vepris*; with tangential or ulmiform pattern towards the outer part of the ring in *Calodendrum* (Fig. 73 K), *Phellodendron*, and *Vepris*; varying in number from 4 to 100 per sq. mm. but mostly between 8 and 40; ring-porous or semi-ring-porous in species of *Acradenia*, *Balfourodendron*, *Calodendrum*, *Choisya*, *Cneoridium*, *Erythrochiton* (1889), *Evodia*, *Phebalium*, *Phellodendron*, *Ptelea*, *Thamnosma*, and *Zanthoxylum*. Spiral

thickening occurs in *Acradenia*, *Asterolasia* (2158), *Calodendrum*, *Choisya*, *Cneoridium*, *Eriostemon* (2158), *Evodia* p.p., *Orixa* (938), *Phebalium*, *Phellodendron*, *Philotheca* (2158), *Poncirus*, *Ptelea*, *Thamnosma*, and *Zieria* (2158). Perforations typically exclusively simple, but a few foraminate plates observed in *Acradenia* and rare reticulate plates in '*Tetractomia*'; Solereder records occasional scalariform plates in some species of *Acronychia*, *Adenandra*, *Agathosma*, *Barosma*, *Boenninghausenia*, *Calodendrum*, *Clausena*, *Leptothyrsa*, and *Paramignya*; modified scalariform plates are also reported (938, 1858) in *Adiscanthus* and *Platydesma*. Intervascular pitting alternate, mostly small to minute, moderately large in *Aegle*, *Aeglopsis*, *Amyris*, *Balsamocitrus*, *Evodia* p.p., *Fagara* p.p., *Murraya*, *Phebalium*, *Phellodendron*, *Ptelea*, *Skimmia*, '*Tetractomia*', and *Zanthoxylum* p.p.; Heimsch (938) notes some scalariform and transitional pitting in *Platydesma* and *Ravenia* *rosa* Standl.; coalescent apertures common in many genera; pits to ray cells and parenchyma similar to the intervascular pitting, occasionally unilaterally compound in *Balfourodendron*, *Citrus* p.p., *Evodia* p.p. and *Poncirus*, and simple in *Orixa* and *Skimmia* (2158); Heimsch notes oblong pits in *Erythrochiton*, *Orixa*, and *Ravenia*; solid deposits common and sometimes abundant. Silica reported in species of *Evodia* (794). Mean member length 0.2–0.6 mm.

Parenchyma absent from *Nethadenia*, present in the other genera as (a) terminal bands, varying from 1 to 6 cells wide, typical of most species, but not observed in *Acronychia* p.p., *Araliopsis*, *Euxylophora*, *Hortia*, *Plethadenia*, and '*Tetractomia*'; (b) paratracheal, predominant in all species, most commonly scanty (Fig. 73 J and L), but aliform to confluent in *Acronychia*, *Afraegle*, *Bosistoa*, *Casimiroa*, *Citrus*, *Clausena excavata* Durand (1154), *Erythrochiton*, *Evodia*, *Fagara* p.p., *Feronia*, *Flindersia* p.p., *Melicope*, *Nycticalanthus*, *Oricia*, *Ravenia*, *Spiranthera*, '*Tetractomia*', and *Zieria*, and connecting the vessels in woods with a pronounced vessel pattern, as in *Acradenia* and *Skimmia*; (c) diffuse, as single strands scattered among the fibres, often consisting almost entirely of chambered crystalliferous cells, present in *Aeglopsis*, *Amyris*, *Araliopsis*, *Balfourodendron*, *Balsamocitrus*, *Bosistoa*, *Calodendrum*, *Chloroxylon* (Fig. 73 H), *Citrus*, *Clausena*, *Evodia* p.p., *Feronia*, *Halfordia*, *Helietta*, *Limonia*, *Melicope*, *Merrillia*, *Murraya*, *Nycticalanthus*, *Oricia*, *Platydesma*, *Poncirus*, *Raputia*, and *Vepris*. Crystals in chambered cells sometimes abundant, observed in the following: *Aeglopsis*, *Afraegle*, *Amyris*, *Araliopsis*, *Atalantia*, *Balfourodendron*, *Balsamocitrus*, *Bosistoa*, *Casimiroa*, *Chloroxylon*, *Citropsis*, *Citrus*, *Clausena*, *Esenbeckia*, *Evodia* p.p., *Fagara*, *Flindersia*, *Halfordia*, *Helietta*, *Limonia*, *Merrillia*, *Murraya*, *Nycticalanthus*, *Oricia*, *Poncirus*, *Spiranthera*, *Teclea*, *Vepris*, and *Zanthoxylum* p.p.; in idio-blasts in *Citrus* p.p. and *Poncirus*. Record and Hess (1889) have reported large bundles of raphides in the diffuse parenchyma of *Raputia magnifica* Engl. Strands typically of 2–4 cells; fusiform cells common in *Plethadenia* (938). Storied in *Chloroxylon* and with a tendency to storied arrangement (echelon) in *Acronychia*, *Balfourodendron*, and *Feronia*. Heimsch (938) reports sclerotic cells in *Flindersia ifflaiana* F. v. Muell. **Rays** exclusively uniseriate in *Amyris*, *Choisya* (occasionally biseriate), *Cneoridium*, *Diosma*, *Merrillia*, *Spiranthera*, and *Thamnosma*; mostly up to 2 or 3 cells wide; up to 6 or more cells wide in some species of *Calodendrum*, *Clausena*, *Esenbeckia* (938), *Evodia*, *Feronia*, *Flindersia*, *Geijera* (938), *Platydesma* (938), and

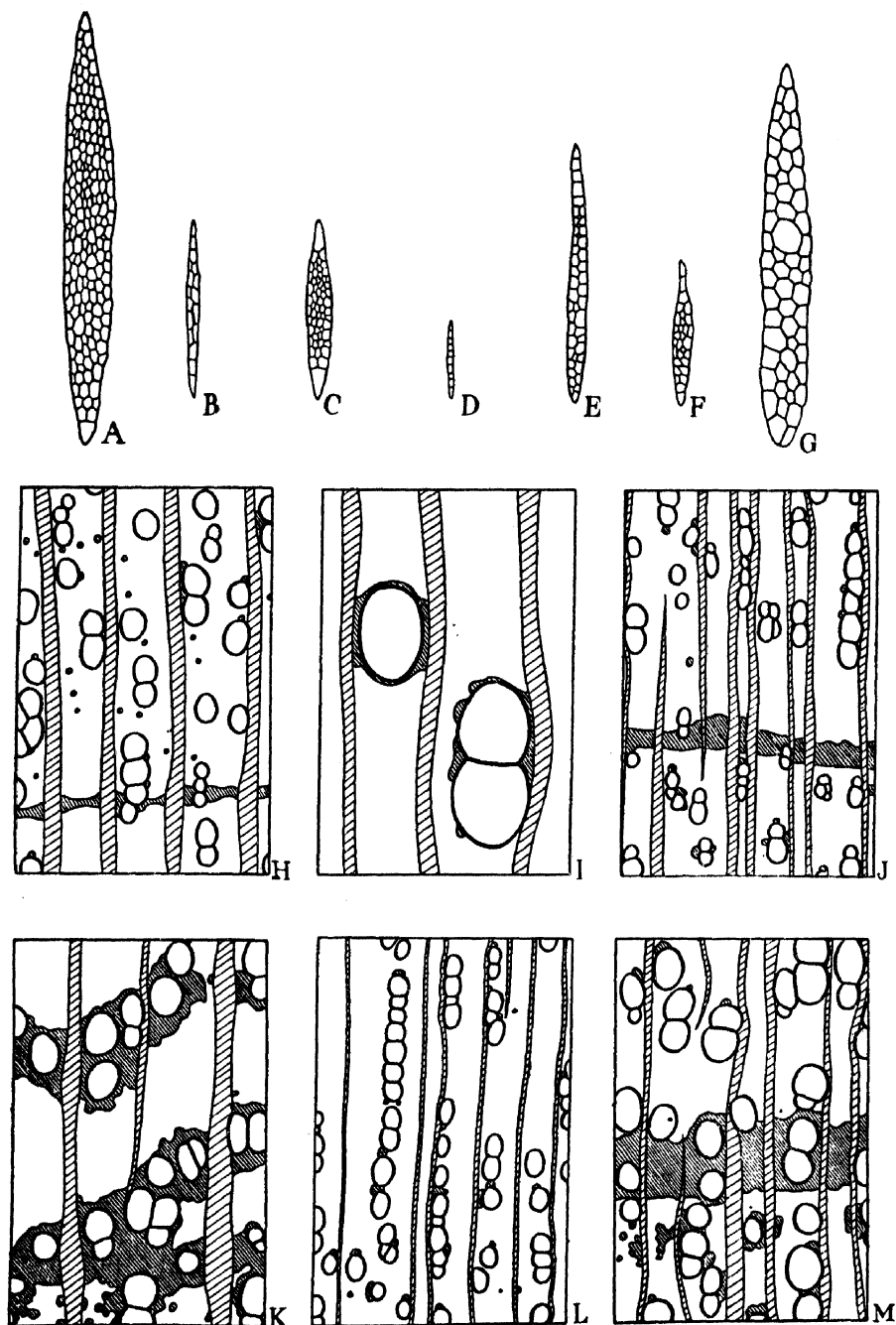


FIG. 73. RUTACEAE

A, *Calodendrum capensis* Thunb. B, *Halfordia scleroxyloa* F. v. M. C, *Chloroxylon swietenia* DC. D, *Amyris balsamifera* Linn. E, *Citropsis articulata* Sw. et Kellerm. F, *Plethadenia cubensis* Urb. G, *Euxylophora paraensis* Huber. H, *Chloroxylon swietenia* DC. I, *Flindersia brayleyana* F. v. M. J, *Teclea simplicifolia* (Engl.) Verdoorn. K, *Calodendrum capensis* Thunb. L, *Amyris balsamifera* Linn. M, *Fagara angolensis* Engl.

Zanthoxylum (938); less than 1 mm. high; uniseriate rays usually scarce or absent from woods with homogeneous or weakly heterogeneous multiseriate rays; between 4 and 14, mostly 7-10, rays per mm.; homogeneous (Kribs's Types I and II) in *Aegle*, *Aeglopsis*, *Afraegle*, *Araliopsis*, *Balsamocitrus*, *Bauerella* (938), *Calodendrum*, *Casimiroa*, *Citrus*, *Cneoridium* (938), *Diosma*, *Euxylophora*, *Fagara* p.p., *Feronia*, *Flindersia*, *Halfordia*, *Helietta*, *Hortia*, *Limonia*, *Merrillia*, *Muraya*, *Oricia*, *Phebalium*, *Phellodendron*, *Plethadenia*, *Raputia*, *Sohnreyia*, *Spiranthera*, *Teclea*, *Vepris*, and *Zieria*, and only weakly heterogeneous in several other genera; typically homogeneous (Kribs's Type III) in the woods with exclusively uniseriate rays, distinctly heterogeneous and sometimes with 4 or more rows of uniseriate marginal cells (not necessarily all square or upright cells) in *Acronychia* p.p., *Atalantia*, *Choisya* (1889), *Citropsis*, *Erythrochiton* (1889), *Esenbeckia*, *Evodia* p.p., *Glycosmis* p.p., *Melicope*, *Metrodorea* (1889), *Micromelum*, *Nycticalanthus*, *Ravenia* (1889), *Skimmia*, '*Tetractomia*', and *Wenzelia* (938); the most unspecialized rays (Kribs's Het. II A), according to Heimsch, occur in the Rutoideae, e.g. in some species of *Erythrochiton*, *Evodia*, *Lunasia*, and *Ravenia*, and in *Rhabdodendron*; with a slight tendency to sheath cells in some species; chambered crystalliferous cells present in *Balfourodendron*, *Balsamocitrus*, *Clausena*, *Chloroxylon*, *Esenbeckia*, *Evodia* p.p., *Feronia*, *Glycosmis*, *Limonia*, and *Micromelum*; silica present in species of *Achroynychia* and *Evodia* (794). Thin-walled oil cells present in *Euxylophora* (Fig. 73 G). Stored in *Chloroxylon* (about 4 per mm.) and in echelon in *Fagara* p.p., *Phellodendron*, *Vepris*, and *Zanthoxylum* p.p. **Fibres** with simple or slightly bordered pits, rare on the tangential walls, few to numerous on the radial walls; Heimsch (938) describes the fibrous elements in *Rhabdodendron* as 'tracheids'; commonly containing gum-like deposits, with numerous small crystals in *Feronia lucida* Scheff.; often septate in *Erythrochiton*, *Phellodendron wilsonii* Hay. et Kanehira (1206) and *Raputia*, and with occasional septa in some species of *Araliopsis* and *Evodia*. Numerous gum plates, some of which are not easily distinguishable from septa, occur in *Flindersia*. Walls moderately thick to very thick, sometimes mucilaginous. Mean length 0.6-1.3 mm. **Tracheids** occur mixed with extremely narrow, often imperfect vessel members in *Acradenia*, *Choisya*, and *Skimmia*. **Intervascular canals** of the traumatic vertical type observed or reported (1889) in *Afraegle*, *Atalantia*, *Balfourodendron*, *Citropsis*, *Citrus*, *Esenbeckia*, *Euxylophora*, *Feronia*, *Fortunella*, *Helietta*, *Hesperethusa*, *Metrodorea*, *Micromelum*, *Pilocarpus*, *Ravenia*, and *Zanthoxylum*. Webber (2377) describes radial intercellular cavities in the rays of *Citrus* trees affected by the physiological disease described as xyloporosis. **Included (interxylary) phloem** reported (938, 1530, 1842) in *Rhabdodendron amazonicum* (Benth.) Hub.; of the 'concentric' type (*c. l. circumvallatum*), with successive development of secondary groups of wood and bast.

ANOMALOUS STRUCTURE, *see* Preceding paragraph

ROOT

Large **idioblasts** with thin, yellow, unligified cell walls and containing resinous material recorded by Brandt (259) in the primary cortex of young roots and in the secondary cortex of older roots of *Ruta graveolens* Linn.

TAXONOMIC NOTES

The wood anatomy of this family is on the whole very uniform and represents a moderately high level of specialization. Heimsch (938) considers that there is strong evidence for considering the Rutaceae, Simarubaceae, Meliaceae, Sapindaceae, Burseraceae, and Anacardiaceae as forming a natural group, with the Rutaceae standing rather apart, owing to its general lack of septate fibres, and showing the closest resemblance to the Simarubaceae.

On the problem of whether *Flindersia* should be placed here or in the Meliaceae, Dadswell (526), Harrar (906), and Record (footnote in Welch 2406) all agree that it is out of place in the Meliaceae owing to its homogeneous rays and non-septate fibres. The genus, however, is variable and, though most species show a greater resemblance to the Rutaceae than to the Meliaceae, there are occasional species, e.g. *F. brayleana* F. v. M. that, except for the presence of gum plates instead of septa in the fibres, are very similar to some species of the Meliaceae, e.g. of *Khaya*. Record suggests that these differences between the species may be of generic rank. Dadswell considers that the genus is not absolutely typical of either the Rutaceae or the Meliaceae and both he and Harrar support the suggestion of a separate family, the Flindersiaceae. The occurrence of secretory cavities and cells in other tissues besides the secondary xylem favours the inclusion of *Flindersia* in the Rutaceae.

The wood anatomy of *Rhabdodendron*, with its bordered pits in the fibres and anomalous structure, appears to be out of place in this family. Record (1842) found little in common between the wood of this genus and that of the Rosaceae, but found a marked affinity with certain genera of the Phytolaccaceae, and Record and Hess (1886) include it in this family.

Hess (950) has drawn attention to a marked dissimilarity between the woods of *Ravenia rosea* Standl. and *R. spectabilis* (Lindl.) Planch.

ECONOMIC USES

The timbers are commonly dense and yellow-coloured and several of them, e.g. *Esenbeckia atata* Pittier, have been used locally or suggested as boxwood substitutes. The Satinwoods are of general commercial importance, the East Indian Satinwood being furnished by *Chloroxylon swietenia* DC. and the West Indian by *Zanthoxylum flavum* Vahl. The timbers of some species of *Flindersia* are among the most important hardwoods of Australia; the wood of *F. brayleana* F. v. M., for example, is used for cabinet work, veneers, aeroplane construction, and rifle stocks, and that of *E. iffaiiana* F. v. M. is reputed to be one of the most important structural hardwoods of north Queensland (525). Pau Marfim, *Balfourodendron riedelianum* Engl., is reported (1084) to be used in Brazil for laminated airscrews.

Apart from the timbers the most important economic products are the Citrus fruits, such as oranges, limes, lemons, grape-fruits, &c. For particulars of the density of stomata and oil glands in the peel of the Washington Naval Orange see the article by Turrell and Klotz (2302); and for the structure of the peel in relation to water spot the account by Scott and Baker (2077). Oil of Rue is distilled from the leaves of *Ruta graveolens* Linn. Various products of medicinal value are also obtained, including Cusparia Bark (*Galipea officinalis* Hancock); Buchu leaves (*Barosma betulina* Bart. and Wendl. and other species of *Barosma*); Jaborandi leaves (*Pilocarpus microphyllus* Stapf and

other species of *Pilocarpus*). Prickly Ash Bark or Toothache Bark is obtained from *Zanthoxylum americanum* Mill. (northern type) and *Z. clava-herculis* Linn. (southern type).

CUSPARIA BARK

The diagnostic anatomical characters are: the cork with the outer tangential walls of the cells strongly thickened; the fairly broad phelloderm consisting of thin-walled cells; the primary cortex containing infrequent groups of strongly thickened yellow fibres and stone cells; the secondary cortex consisting mostly of thin-walled tissue arranged in alternating layers of parenchyma and disorganized sieve elements and traversed by rays 1-3 cells wide; the secretory cells, raphides, other crystals, and starch. Copalchi Bark (*Croton niveus* Jacq.) (see Euphorbiaceae) and Angusturo Bark (*Esenbeckia febrifuga* A. Juss.) are sometimes used as substitutes. Angusturo bark may be recognized by the 3 or 4 layers of colourless cells in the inner part of the cork, which are capable of being stained bright blue by acids with oxidizing properties, owing to the presence of the alkaloid evodin.

BUCHU LEAVES

The diagnostic anatomical characters are: the epidermis on both surfaces composed of cells with straight anticlinal walls; abundant mucilage in the epidermis and hypoderm; dendritic crystals of diosmin, which occur especially in the epidermis; the large oil glands and cluster crystals of calcium oxalate in the mesophyll; the single layer of palisade tissue; the ranunculaceous stomata, confined to the lower surface.

The leaves of *B. betulina* Bart. et Wendl. can frequently be distinguished from those of other species of *Barosma* which are used as substitutes by a proportion of the stomata being more than $38\ \mu$ in diameter. Levin (1366) has shown how differences in the vein-islet numbers may also be used to distinguish *B. betulina* and *B. crenulata* (L.) Hook. from other species of *Barosma* (*B. betulina* 10-15 (average 12.7) and *B. crenulata* 10-16.5 (average 13) per sq. mm., but varying somewhat in the last of these species). The anatomy of an unidentified adulterant of Buchu has been described by Small (2133).

JABORANDI LEAVES

The diagnostic anatomical characters are: the epidermis on both surfaces composed of mostly pentagonal and hexagonal cells with practically straight anticlinal walls; the stomata confined to the lower surface, each surrounded by 4 or 5 concentric subsidiary cells; the single layer of palisade tissue; the broader region of spongy tissue; the large secretory cavities, the scattered secretory cells with reddish-brown contents, and the cluster crystals of calcium oxalate, all of which occur in the mesophyll; the circular vascular strand of the midrib surrounded by thick-walled fibres.

PRICKLY ASH BARK

The diagnostic anatomical features of the bark of *Zanthoxylum americanum* Mill. are: the narrow, easily detached cork consisting of about 4 layers of brownish thick-walled, tabular cells, stained golden orange when treated with iodine; the cortex composed of tangentially elongated, parenchymatous cells, in many of which there are solitary, prismatic crystals; the broader phloem, traversed

by narrow medullary rays; the thick-walled secretory cells with oily contents, which are rounded or oval in transverse sections but somewhat elongated longitudinally and occur in the cortex and, more abundantly, in the phloem; the amorphous and oily material deposited chiefly in most of the ray cells and some of the cortical cells; the sporadic small bundles of fibres and chains or clusters of stone cells, both stained golden yellow by iodine, which occur in the cortex; the abundant crystals attached to the inner surface of the bark.

It has been claimed by Wirth (2447) that the bark of *Z. clava-herculis* Linn. can often be distinguished from that of *Z. americanum* by the absence of crystals from the inner surface of the bark of the first of these species.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acmadenia, Adenandra,* Agathosma,* Almeidea, Amyris, Asterolasia, Balsamocitrus, Barosma,* Boenninghausenia, Boronia,* Calodendrum,* Casimiroa,* Choisyia,* Chorilaena, Citrus,* Clausena, Cneoridium, Coleonema,* Correa,* Crowea,* Cusparia, Dictamnus,* Dictyoloma, Diosma, Diplolaena, Empleurum, Eremocitrus, Eriostemon,* Erythrochiton, Esenbeckia, Euchaetis, Evodia,* Flindersia, Galipea, Macrostylis, Melicope,* Metrodorea, Monnieria, Murraya,* Nematolepis, Orixia,* Pagetia, Paramignya, Peganum,* Phebalium, Phellodendron,* Pilocarpus,* Poncirus,* Ptelea,* Raputia, Ravenia,* Ruta,* Skimmia,* Spiranthera, Toddalia,* Zanthoxylum,* Zieria.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Acradenia, Acronychia, (Adiscanthus), Aegle, Aeglopsis, Afraegle, Araliopsis, Atalantia, Balsamocitrus, (Bauerella), Bosistoa, Calodendrum, Casimiroa, Choisyia, Citropsis, Citrus, Clausena, (Clausenopsis), Cneoridium, (Dictyoloma), Diosma, Erythrochiton, Esenbeckia, Euxylophora, Evodia, Fagara, Feronia, Flindersia, (Fortunella), (Geijera), Glycosmis, Halfordia, Helietta, (Hesperethusa), Hortia, Limonia, (Medicosma), Melicope, Merrillia, Metrodorea, (Microcitrus), Micromelum, Murraya, Nycticalanthus, Oricia, (Orixa), (Paramignya), (Pelea), Phebalium, Phellodendron, (Pilocarpus), Platydesma, Pleiococca, Plethadenia, Poncirus, Ptelea, Raputia, Ravenia, (Rhabdodendron), Skimmia, Sohnreyia, Spiranthera, (Swinglea), Teclea, 'Tetractomia', Thamnosma, Vepris, Zanthoxylum, Zieria.

LITERATURE

(i) On General Anatomy

Brandt 259, Butler 324, Crossman 511, Elias 625, Engler 641, Hirano 979, Holm 999, Klein and Bartosch 1245, Levin 1366, Livingstone 2526, McLean 1468, Reed 1897, Scott 2532, 2533, Scott and Baker 2077, Shelton 2086, Small 2133, Swingle 2225, Turrell 2301, Turrell and Klotz 2302, Wirth 2447, Wood, J. G. 2457.

(ii) On Wood Structure

Baker 104, den Berger 179, 182, Besson 186, Brit. Hond. F. D. 274, Brown, F. B. H. 282, Burgerstein 310, 312, Cockrell 435, Cooper 461, Coster 481, Dadswell 524, 525, 536, Foxworthy 705, Giordano 786, Gonggrijp 794, Greguss 2522, Harrar 906, Heimsch 938, Hess 950, Horn 1084, Howard 1088, Janssonius 1154, Jolly 1188, Kanehira 1206, 1209, Lecomte 1334, Metcalfe 1497, Milanez 1530, Pearson and Br. 1679, Pereira 1687, Pfeiffer J. Ph. 1713, Record 1780, 1781, 1787, 1801, 1809, 1842, 1843, 1851, 1884, Record and Hess 1886, 1889, Record and Mell 1894, Scott 2075, Stone 2202, Sudworth 2218, Tang 2231, Webber 2377, Welch 2406, 2408, Williams 2430, Yamabayashi 2478.

✓ 80. SIMARUBACEAE

(FIG. 74 on p. 318; FIG. 75 on p. 322; FIG. 77 on p. 334)

SUMMARY

(i) GENERAL

Trees or shrubs which occur chiefly in tropical countries. The **hairs** are mostly simple, unicellular or uniseriate. Glandular hairs, sunken glands, and extra-floral nectaries also occur in certain genera and species. The **leaf** is usually dorsiventral, rarely isobilateral or sub-centric. The **epidermis** is frequently mucilaginous and sometimes papillose. **Stomata**, mostly confined to the lower surface, are usually ranunculaceous, except in a few genera in which they are rubiaceous. Various shaped, sclerenchymatous idioblasts are common in the **mesophyll**. The **petiole**, in transverse sections through the distal end, usually exhibits a cylindrical vascular strand which, in certain genera, encloses medullary bundles, whose orientation and distribution have been used in the identification of species. In the young stem the **cork** is usually superficial in origin; the **pericycle** is bounded by isolated strands of fibres or a composite and continuous ring of sclerenchyma; the **xylem** and **phloem** form continuous cylinders. **Secretory canals** occur in certain genera especially in the peripheral region of the pith, whence they extend via the petiole to the major leaf veins. **Secretory cells** containing oil, resin, or mucilage, although less common, are to be found in the parenchymatous tissues.

(ii) WOOD

This family includes a wide variety of anatomical features, but it has been shown by Webber (2374) that this is largely due to dissimilarity between some of the tribes.

Vessels evenly distributed in most genera, but with a radial or oblique pattern in some; a few species definitely or slightly ring-porous; perforations exclusively simple, with a few minor exceptions; intervascular pitting alternate, varying from very small to large; pits to ray cells and parenchyma similar to the intervascular pitting in most species but large and tending to be simple in some; members of medium length to moderately short. **Parenchyma** extremely variable, ranging from extremely sparse or absent to abundant, in broad bands; usually with at least some parenchyma associated with the vessels; diffuse parenchyma or fine metatracheal bands, predominant in a few species and diffuse parenchyma sometimes present in woods with predominantly paratracheal parenchyma; terminal parenchyma sometimes present. Storied in several species. **Rays** multiseriate except in 1 genus, usually between 2 and 4 cells wide, larger in *Ailanthus*; commonly homogeneous, occasionally distinctly heterogeneous; often storied. **Fibres** with small simple or bordered pits; sometimes septate; of medium length. **Vasicentric tracheids** present in a few species. **Vertical intercellular canals**, probably traumatic, often present.

LEAF

Usually dorsiventral, but sometimes isobilateral or centric (see 'Mesophyll'). **Hairs** unicellular or uniseriate, mostly sclerenchymatous. Stalked glands

(Fig. 74 A-B) occur in *Ailanthus*, *Alvaradoa*, *Brucea*, *Harrisonia*, *Hebonga*, *Picramnia*, *Rigiostachys*, *Simaba*, *Simaruba*, *Soulamea*, *Suriana*, but are generally infrequent except in *Suriana*. Shaggy glands recorded in *Eurycoma* (Fig. 74 C), and large, conspicuous, wart-like glands on the teeth at the base of the leaflets of *Ailanthus altissima* Swingle (syn. *A. glandulosa* Desf.).

Sugar is stated by Petaj (1700) to be secreted from the so-called nectar tissue of the glands of *Ailanthus altissima* directly through the epidermis, no special secretory channels being present. Exudation, which does not appear to be correlated with insect visits, begins as soon as the bud unfolds; is most active in the early morning and slows down during the course of the day. More recently the glands of *Ailanthus* have been studied by Davis (551).

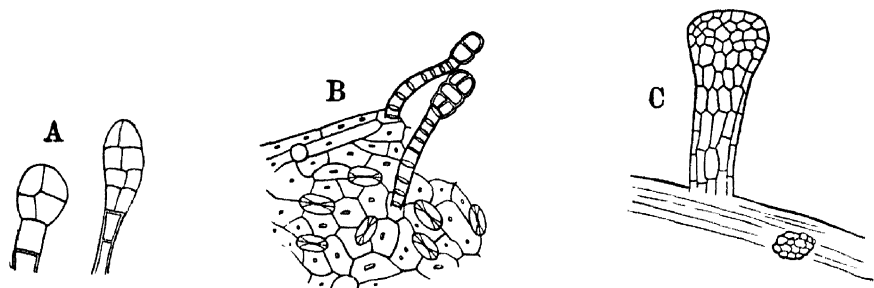


FIG. 74. SIMARUBACEAE

Hairs of A, *Picramnia* sp. B, *Rigiostachys bracteata* Planch. C, *Eurycoma longifolia* Jack.—By Solereder.

Extra-floral nectaries, in the form of sunken glands, also occur on various parts of the leaf in numerous genera. (i) On the lower surface of the lamina in *Alvaradoa*, *Brucea*, *Eurycoma*, *Harrisonia*, *Picramnia*. (ii) On the upper surface of the lamina in *Cadellia*, *Hannoa*, *Odyndea*, *Simaba*, *Simaruba*. (iii) Confined to the apex and base of the lamina in certain species of *Hannoa*, *Mannia*, *Simaba*, *Simaruba*, and *Simarubopsis*. (iv) On the petiole in *Cadellia*. Extra-floral nectaries stated to be absent from the Irvingeeae and from *Castela*, *Hebonga*, *Kirkia*, *Picrasma*, *Quassia*, and *Rigiostachys*. **Epidermis** single-layered in most genera, but cells sometimes becoming septate in *Amaroria*, *Castela*, *Hannoa*, *Soulamea*. True **hypoderm** recorded by Solereder and by Spiekerkoetter (2168) only in certain species of *Ailanthus* and *Odyndea*. Lower epidermis papillose in certain species of *Ailanthus*, *Alvaradoa*, *Desbordesia*, *Eurycoma*, *Irvingella*, *Irvingia*, *Klainedoxa*, *Odyndea*, *Simaruba*. Epidermal cells mucilaginous in species of *Ailanthus*, *Alvaradoa*, *Castela*, *Hannoa*, *Harrisonia*, *Hebonga*, *Kirkia*, *Mannia*, *Odyndea*, *Picrasma*, *Simaruba*, *Simarubopsis*, as well as in all of the Irvingeeae and Soulameae; less frequently mucilaginous in *Brucea*, *Cadellia*, *Eurycoma*, *Guilfoylia*, *Picramnia*, *Picrasma*, *Picrolemma*, *Quassia*, *Rigiostachys*, *Samadera*, *Simaba*. **Stomata** very numerous and almost exclusively confined to the lower surface, but present on the upper surface as well in *Suriana maritima* Linn. and sporadically, especially near the veins, in a few species of *Ailanthus*, nearly always at the same level as the surrounding epidermal cells; ranunculaceous, usually surrounded by 4-10 ordinary epidermal cells, but rubiaceae types recorded in *Castela*, *Irvingia*, *Klainedoxa*, and *Picrodendron*. Three to five epidermal cells surround the stomata in *Suriana*, and sometimes exhibit a well-marked cruciferous

arrangement when each stoma is surrounded by 3. Stomata in groups in *Castela* and *Soulamea*, and tending to be in parallel groups of about 5 in *Irvingia* and less frequently in *Klainedoxa*. Peculiar processes are stated to be present at either end of each stoma throughout most of the genus *Picramnia*. **Mesophyll** typically dorsiventral, but somewhat variable; centric in certain species of *Ailanthus*, *Castela*, and *Suriana*; isobilateral or sub-centric in *Harrisonia abyssinica* Oliv. according to Spiekerkoetter (2168) and in *Kirkia*; usually homogeneous and palisade-like in the Irvingiae as well as in *Cadellia* and *Picrodendron*. Palisade tissue consisting of 1–3 layers; cells described by Spiekerkoetter (2168) as transversely septate in *Amaroria*, *Harrisonia* sp., *Soulamea*, and in certain of the Irvingiae. Spongy parenchyma usually fairly lacunar; consisting of hypha-like cells in *Eurycoma*, *Simaba*, *Simaruba*, *Simarubopsis*. Sclerenchymatous idioblasts, which exhibit a wide range of form and variations in the thickness of the cell wall, occur in the mesophyll throughout *Eurycoma*, *Hannoa*, *Hyptiandra*, *Mannia*, *Odyndea*, *Perrieria*, *Quassia*, *Simaba*, *Simaruba*, *Simarubopsis*. Those which are to be found in certain species of *Irvingella*, *Irvingia*, *Picramnia*, *Picrasma*, and *Samadera* extend from the fibres around the bundles and end blindly in the mesophyll. Small, infrequent idioblasts sometimes occur in other genera besides those listed above; none recorded for *Harrisonia* and *Klainedoxa*. **Veins** very prominent in *Soulamea* owing to the development of collenchyma on both sides of the leaf, and in *Castela* owing to the presence of palisade tissue in the corresponding position. Elsewhere, veins generally embedded in the mesophyll; provided with well-developed parenchymatous sheaths in *Cadellia*, *Kirkia*, *Picrasma*, *Simaba*, *Simaruba*, *Simarubopsis*, *Soulamea* (cells containing brown tannic material), *Suriana*. Small veins vertically transcurrent in *Irvingia*, *Klainedoxa*, and *Picrodendron*. **Petiole**, in transverse sections through the distal end, exhibiting a closed, circular vascular strand surrounding a number of variously orientated medullary bundles in many species. Medullary bundles recorded in the petiole of *Ailanthus* (Fig. 77 L), *Amaroria*, *Hebonga*, *Picrasma*, *Picrolemma*, *Quassia*, *Samadera*, *Simaba*, *Simaruba*, *Soulamea*, and possibly other genera as well; absent from at least certain species of *Aeschrion* (Fig. 77 I), *Alvaradoa*, *Brucea*, *Castela*, *Harrisonia*, *Irvingia*, *Klainedoxa*, *Picramnia*, *Picrodendron*. Orientation and number of medullary bundles stated by Solereder to be of specific diagnostic value. Petiole containing a single arc-shaped bundle in *Suriana*, and a closed or dissected annular bundle in *Rigiostachys*. **Secretory canals** frequently accompany the vascular bundles of the veins, especially in those genera where they occur in the axis also (see 'Young Stem'). **Oil cells** recorded by Engler (642) in the parenchymatous portions of the leaf in *Picrella trifoliata* H. Baill. and in all species of *Ailanthus*, *Harrisonia*, *Hebonga*, *Simaba*, *Simaruba*, and **mucilage cells** and cavities throughout *Desbordesia*, *Irvingia*, and *Klainedoxa*. **Crystals** solitary or clustered. Cluster crystals the commonest type, very variable in size, particularly large in *Castela*, *Holacantha*, *Picramnia*; their size and distribution are said to be of value in the identification of genera (for details see Boas's (208) article). Solitary crystals especially frequent in the Irvingiae. Sphaerites recorded in *Picramnia* and *Suriana*. Styloids confined to *Alvaradoa*. A substance resembling **hesperidin** recorded in certain species of *Irvingella*. Ash containing 0.698 per cent. of copper in *Odyndea gabunensis* (Pierre) Engl.

AXIS

YOUNG STEM (Fig. 77 M)

Stomata deeply sunken in the leafless *Holacantha emoryi* A. Gray. **Cork** usually arising in the sub-epidermis except in the Irvingiae and in *Amaroria*, *Rigiostachys*, *Soulamea*, and *Suriana*. Cork cells with U-shaped thickenings recorded in certain species of *Irvingella*, *Irvingia*, and *Klainedoxa*. **Cortex** sometimes containing stone cells, notably in species of *Castela*, *Quassia*, *Samadera*, *Simaruba*. Inner part of the cortex strongly collenchymatous in *Aeschrion excelsa* (Sw.) Kunze (syn. *Picraena excelsa* Lindl.). **Pericycle** sometimes containing isolated strands of fibres (e.g. with a broad but interrupted ring in *Aeschrion excelsa* and *Picrasma quassioides* (Ham.) Benn.), but with a composite ring of sclerenchyma in certain species of *Ailanthus*, *Alvaradoa*, *Cadellia*, *Castela*, *Picramnia*, *Quassia*, slightly interrupted in *Q. amara* Linn., *Rigiostachys* (ring becoming broken into groups with increase in age), *Samadera*. Pericycle sometimes devoid of sclerenchyma in *Holacantha*, but sub-epidermal groups of fibres separated by palisade-like assimilatory tissue occur in this genus. **Xylem** and **phloem** constituting closed cylinders, but primary rays fairly conspicuous, e.g. in *Ailanthus* (Fig. 77 M). Vessels usually with simple perforations. Sclerenchymatous elements often present in the primary and especially in the secondary phloem, notably in species of *Brucea*, *Harrisonia*, *Simaba*, and *Simaruba*. **Pith**, described by Spiekerkoetter (2168) as heterogeneous, consisting of small, thick-walled cells distributed amongst larger cells with thin walls in *Harrisonia*. Medullary **secretory canals**, often closely associated with the protoxylem, and very variable in number and size, recorded in certain species of *Ailanthus*, *Amaroria*, *Brucea*, *Eurycoma*, *Hannoa*, *Mannia*, *Odyndea*, *Perrieria*, *Picrasma*, *Picrella*, *Picrocardia*, *Picrolemma*, *Samadera*, *Simaba*, *Simaruba*, *Simarubopsis*, *Soulamea*. Secretory canals apparently absent from species of *Alvaradoa*, *Cadellia*, *Castela*, *Eurycoma*, *Guilfoylia*, *Hannoa*, *Harrisonia*, *Holacantha*, *Hyptiandra*, *Irvingia*, *Kirkia*, *Klainedoxa*, *Picramnia*, *Picrasma*, *Picrodendron*, *Quassia*, *Rigiostachys*, *Samadera*, *Simaba*, *Spathalea*, *Suriana*. The presence or absence of medullary secretory canals is usually a character of generic diagnostic value, although exceptions occur, notably in *Simaba*, where a group of species with and another without canals was distinguished by Boas (208). Canals recorded in the cortex in certain species of *Harrisonia* and *Irvingia*, and also in the pericycle in *Odyndea* sp. **Secretory cells** also frequent in the cortex and pith, either alone or accompanied by canals. Oil cells recorded by Engler (642) in the cortex and pith of *Picrella trifoliata* H. Baill. and in the same tissues throughout *Ailanthus*, *Harrisonia*, *Hebonga*, *Simaba*, *Simaruba*, and mucilage cells and cavities in all species of *Desbordesia*, *Irvingia*, and *Klainedoxa*. Secretory elements generally absent from the Alvaradoideae, Castelineae, Eurycomineae, Kirkieae, Picramnioideae, and Surianoideae. *Simaruba* is sharply differentiated from *Simaba*, according to Solereder, by the presence of secretory cells in the axis, petiole, and lamina. Solitary and clustered **crystals** common; small solitary ones occur in the cortex of *Ailanthus altissima* Swingle and druses, sometimes very large, in the cortex of *Picrasma quassioides* (Ham.) Benn.

BARK

Structure fully described for *Ailanthus altissima* Swingle by Müller (1572) as follows. Cork consisting of flattened, compact cells, with strongly thickened inner walls. Phelloderm consisting of tangentially elongated cells. Cork and phelloderm cells with homogeneous contents. Phelloderm also containing small starch grains and large cluster crystals. Phloem including conspicuous groups of fibres and solitary or, more frequently, grouped, tangentially elongated cells with brown resinous contents. Medullary rays 1–3 cells wide, consisting of thin-walled, radially stretched cells.

WOOD (Fig. 75)

Vessels mostly medium-sized (100–200 μ mean tangential diameter) in diffuse-porous species, larger in some species of *Ailanthus*, *Hannoa*, *Klainedoxa*, *Odyndea*, and *Simaruba*, smallest in *Alvaradoa*, *Brucea*, *Guilfoylia*, *Picraena*, *Quassia*, *Samadera*, and *Suriana*; pore multiples not very common in most species but multiples of 4 or more moderately common in *Castela*, *Guilfoylia* (Fig. 75 I), *Picramnia*, and *Suriana* (2374); clusters present in the foregoing genera and in *Brucea* and *Picraena*; in clusters of very small, often angular, vessels in the late wood of *Ailanthus altissima* Swingle, the clusters often grouped into tangential lines (Fig. 75 J); tending to a flame-like or oblique distribution in *Alvaradoa*, *Castela*, and *Holacantha* (938); varying in number from 1 to 5 per mm. in the woods with larger vessels, not more than 20 per mm. in the remainder (excluding woods with marked groups of vessels); ring-porous in some species of *Ailanthus*, *Holacantha* (938) and *Picrasma* (938, 2374), semi-ring-porous in some species of *Alvaradoa* and *Castela*. Spiral thickening present in the smaller vessels of *Ailanthus altissima* and in *Castela nicholsonii* Hook. f. (2374), *Holacantha emoryi* A. Gray (2374), and *Picramnia* (938). Perforations exclusively simple, except for occasional multiple perforations in the late wood of *Ailanthus altissima* (2374). Intervascular pitting alternate, often wider horizontally than vertically, including a wide range of size, large (7–10 μ diam.) in *Ailanthus*, *Guilfoylia*, *Hannoa*, *Irvingia*, *Kirkia*, *Klainedoxa*, *Odyndea*, *Samadera*, and *Simaruba*, small to minute in *Alvaradoa*, *Brucea*, *Castela*, *Picraena*, *Picramnia*, and *Quassia*; sometimes with coalescent apertures—most pronounced in *Hannoa*, *Picraena*, *Picramnia*, and *Simaruba*; sometimes transitional in *Kirkia acuminata* Oliv.; pits to ray cells similar to intervacular pits where these are small, large, unilaterally compound or simple in woods with large intervacular pitting, e.g. in *Hannoa*, *Irvingia*, *Klainedoxa*, and *Samadera*. Tyloses abundant; sometimes containing gum and crystals in *Kirkia* (2374). Mean member length 0.3–0.7 mm. **Parenchyma** very sparse in or absent from *Guilfoylia* and *Picramnia*, vasicentric in *Brucea*, *Dictyoloma*, *Holacantha*, and *Kirkia*, aliform or confluent in *Aeschron*, *Ailanthus*, *Castela*, *Hannoa* (Fig. 75 F), *Irvingia*, *Klainedoxa*, *Odyndea*, *Picrasma*, *Quassia*, *Simaba*, and *Simaruba*, in continuous bands, probably but not obviously paratracheal in origin, in *Castela*, *Hannoa*, *Irvingia* (Fig. 75 K), and *Klainedoxa*; also banded, according to Heimsch, in *Amaroria*, *Cadellia*, *Desbordesia*, *Eurycoma*, and *Soulamea*; diffuse or fine metatracheal bands predominating in *Samadera*, and present in addition to paratracheal parenchyma in *Cadellia* (2374), *Castela*, *Harrisonia* (938), *Klainedoxa*, *Mannia* (938), *Picrodendron* (938), and *Suriana* (2374);

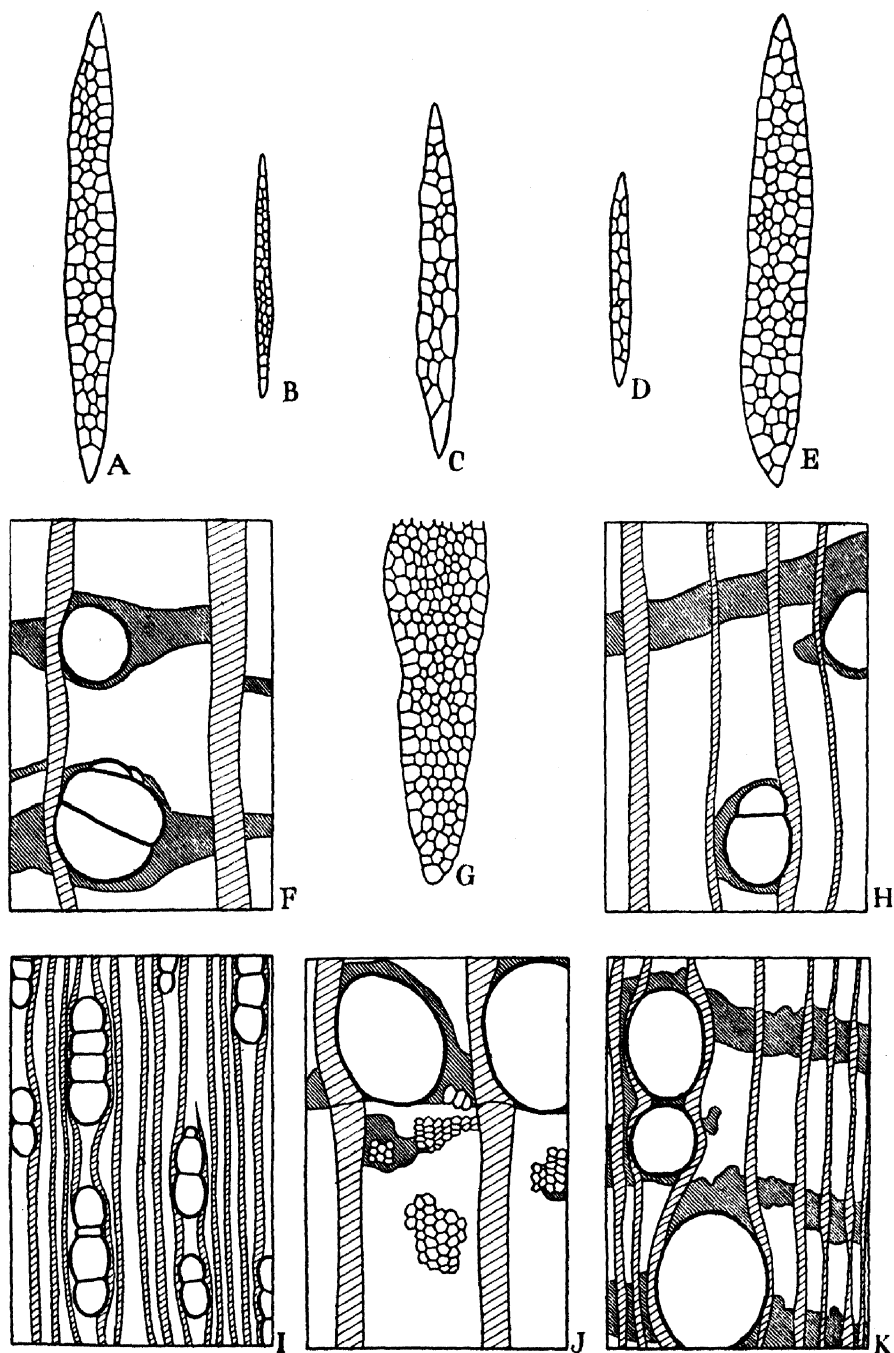


FIG. 75. SIMARUBACEAE

A, *Kirkia acuminata* Oliv. B, *Irvingia gabonensis* Baill. C, *Brucea macrophylla* Oliv. D, *Odyndea zimmermannii* Engl. E, *Hannoa klaineana* Pierre et Engl. F, *H. klaineana* Pierre et Engl. G, *Ailanthus altissima* Swingle. H, *Simaba multiflora* Juss. I, *Guilfoylia monostylis* (Benth.) F. Müll. J, *Ailanthus altissima* Swingle. K, *Irvingia gabonensis* Baill.

terminal parenchyma present in some species, e.g. of *Amaroria*, *Cadellia*, *Holacantha*, and *Simaba*. Crystals present in the majority of species either in the ordinary cells (large in *Alvaradoa*) or in chambered cells, not abundant except in *Hannoa undulata* Pierre et Engl., *Irvingia*, *Klainedoxa*, and *Suriana* (2374). Storied in *Ailanthus* p.p., *Cadellia* (2374), *Castela*, *Picrasma*, *Simaba*, *Simaruba*, and *Suriana* (2374). Strands usually of 2-4 cells, but commonly up to 8 cells and sometimes more in *Irvingia*, *Kirkia*, and *Klainedoxa*. **Rays** exclusively uniseriate in *Aeschrion*, *Guilfoylia*, and *Quassia*; mostly 2-4 cells wide in the other genera, but occasionally, according to Heimsch, up to 7 cells wide in *Alvaradoa*, *Castela*, *Holacantha*, *Picrasma*, and *Simaruba*; larger and sometimes more than 10 cells wide in *Ailanthus*; more than 1 mm. high in *Ailanthus*, *Brucea*, *Guilfoylia*, and *Samadera*; uniseriates typically few and composed of procumbent cells, but numerous and composed of upright cells in *Picramnia* and *Samadera*, and of a few upright to procumbent cells in *Alvaradoa* and *Brucea*; rays varying in number from about 4 per mm. in some species of *Ailanthus*, *Kirkia*, *Odyndea*, and *Picrasma*, to about 17 per mm. in *Aeschrion*, *Cadellia* (2374), *Guilfoylia*, *Mannia* (2374), and *Samadera*, and up to 29 per mm. in *Suriana* (2374); homogeneous (Kribs's Types I, II, and III) in *Aeschrion*, *Ailanthus*, *Amaroria* (938), *Cadellia* (938), *Castela*, *Desbordesia* (938), *Eurycoma* (938), *Hannoa*, *Holacantha*, *Irvingia*, *Klainedoxa*, *Odyndea*, *Picrasma*, *Quassia*, *Simaba*, *Simaruba*, and *Soulamea*; markedly heterogeneous (Kribs's Type II A), with 4 or more marginal rows of square or upright cells, in *Brucea*, *Picramnia*, and *Samadera* and, according to Heimsch (938), in *Alvaradoa*; Heimsch (938) lists the following as having moderately heterogeneous rays (Kribs's Type II B): *Aeschrion* p.p., *Brucea*, *Harrisonia*, *Holacantha*, *Irvingia*, *Kirkia*, *Mannia*, *Picrodendron*, and *Simaba*; cells in most species wider vertically than transversely as seen in tangential sections. Occasional crystals present in the ordinary cells in some species, but not numerous, and in chambered cells in *Samadera*; cells containing dark gum in *Irvingia* and *Kirkia*, and gum reported by Webber (2374) as sometimes present in *Alvaradoa*, *Cadellia*, *Picramnia*, and *Suriana*. Cell walls thin to very thin in some species, particularly in *Brucea*, *Odyndea*, and *Simaruba* and with small, but numerous, intercellular spaces in *Brucea*, *Castela*, *Hannoa*, *Odyndea*, *Samadera*, and *Simaruba*. Pits between ray cells small and very numerous in *Picrasma*. Storied in some species of *Aeschrion*, *Castela*, *Hannoa* (2374), *Odyndea* (2374), *Picrasma*, *Quassia*, *Simaruba*, and *Soulamea* (2374), and occasionally with a tendency to stories in some specimens of *Kirkia*. **Fibres** with simple or bordered pits, more numerous on the radial than on the tangential walls, except in *Irvingia* and *Kirkia*; borders, when present, usually small and inconspicuous but moderately distinct in *Ailanthus* and *Simaruba*; Webber (2374) distinguishes the following woods as having fibre-tracheids, *Alvaradoa*, *Picramnia*, and all the genera of the sub-family Simaruboidae other than *Castela* and *Holacantha*. Commonly septate in *Alvaradoa* and *Kirkia*, the septate fibres of the former grouped in zones or patches; occasionally septate in *Ailanthus malabarica* DC. (1334), *Guilfoylia*, *Picramnia*, *Soulamea fraxinifolia* Brongn. et Gris., *S. muelleri* Brongn. et Gris. (2374), and *Suriana* (2374); lumina occasionally filled with gum in *Suriana* and *Cadellia* (2374); walls thick in *Castela*, *Guilfoylia*, *Holacantha*, *Irvingia*, and *Klainedoxa*. Mean

length 0.9–1.7 mm. **Vasicentric tracheids** reported by Webber (2374) in *Alvaradoa*, *Castela*, and *Holacantha*; those of *Alvaradoa* with spiral thickening (938). **Intercellular canals.** Vertical intercellular canals occur normally near the protoxylem of many species of this family (see p. 320). Vertical canals have also been observed in the secondary wood of many of these species, but appear to be traumatic, though Record (1843) classifies those occurring in *Simaruba* as normal. Webber (2374) reports such canals in *Ailanthus altissima*, *A. philippinensis* Merr., *Castela nicholsonii*, *Eurycoma longifolia* Jack, *Picraena paloamarga* (Speg.) Soeg., *Simaruba amara* Aubl., and *Soulamea amara* Lam., and Heimsch (938) in *Brucea macrophylla* Oliv. The canals vary considerably in size. Gummosis of unusually broad multiserate rays has been reported in *Odyndea ovalis* A. Peter (2168) and in *Ailanthus altissima* and *Klainedoxa gabonensis* Pierre (2374).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

There are very few anatomical characters common to the whole of the Simarubaceae. This lack of homogeneity, which occurs also in the external morphological characters, seems to indicate that the family is unnatural, but consists of a number of groups which are themselves relatively uniform. It was pointed out by Jadin (1138) that, on anatomical grounds, the Irvingiae are clearly differentiated from the Simarubaeae. He also suggested, although on somewhat inadequate anatomical grounds, that *Suriana* should form the basis of a separate family, the Surianaceae, having affinities with the Geraniaceae. It is interesting to note that *Brunellia*, which was included in the system of Bentham and Hooker amongst the Simarubaceae, differs from most other members of the family which have been investigated anatomically in the possession of a mixture of simple elliptical perforations and scalariform perforation plates to the vessels. *Brunellia* has, since then, on external morphological evidence, been transferred to a separate family placed by Engler and Hutchinson in their respective systems near the Cunoniaceae, where similar vessel perforations also occur. Reference to the description of the Cneoraceae will show that its members exhibit quite notable differences from the Simarubaceae, so that its separation into a distinct family seems to be fully justified. *Koeberlinia*, which was included in the Simarubaceae in the Bentham and Hooker system, was described under Cappariaceae by Pax and Hoffman (1678). On anatomical grounds it does not agree very well with either family, and there seem to be good reasons for treating it separately as the Koeberliniaceae.

(ii) FROM WOOD STRUCTURE

The systematic anatomy of the woods of this family has been investigated by Webber (2374), who has drawn the following conclusions. Each of the sub-families Kirkioideae, Irvingioideae, and Alvaradoideae represents a distinct, homogeneous group, whereas the Surianoideae shows some divergence and the Simaruboideae exhibits somewhat wide variation. The structure of the Surianoideae supports Solereder's abolition of the monotypic family Surianaceae, his close grouping of *Suriana* and *Cadellia*, and his withdrawal of *Guilfoylia* from *Cadellia*. Within the Simaruboideae, the structure

of *Holacantha* and *Castela* differs markedly from that of all other genera. However, the difference does not support Jadin's erection of the monotypic family Holacanthaceae, since *Castela* resembles *Holacantha*. The genus *Picrodendron*, formerly included in the Irvingioideae, bears considerable resemblance to the members of this sub-family in wood structure.

The wood anatomy of the sub-families Kirkioideae, Irvingioideae, Picramnioideae, and Alvaradoideae might support the ranking of these groups as distinct families or as components of other families if this were suggested on other morphological grounds.

Heimsch (938) in general supports Webber's conclusions. Record and Hess (1886) place *Picrodendron* apart in the Picrodendraceae and *Suriana* in the Surianaceae, and comment that the classification of the family would be simplified still further by excluding *Alvaradoa* and *Picramnia*.

ECONOMIC USES

Quassia chips *Aeschron excelsa* (Sw.) Kuntze (syn. *Picraena excelsa* Lindl.) possess tonic and anthelmintic properties. This material is also used in the preparation of insecticides. The West African Dika Nut consists of the kernels of *Irvingia gabonensis* Baill. The powdered leaflets of *Ailanthus altissima* Swingle (syn. *A. glandulosa* Desf.) have sometimes been used as an adulterant in belladonna, mint, and other leaves which occur in commerce. *Ailanthus* leaves may often be detected by the presence of the characteristic glands (see 'Leaf'), but other diagnostic characters include the striated cuticle; the large unicellular trichomes; the clustered crystals which accompany the veins; the ranunculaceous stomata; the single layer of palisade cells; the straight anticlinal walls of the epidermal cells. None of the genera furnishes timber of general commercial importance, though some, e.g. *Ailanthus* and *Simaruba*, produce timber that is used locally, chiefly for packing-cases.

According to Record and Hess (1886) limited amounts of Marupá (believed to be *Simaruba amara* Aubl.) have been exported from Brazil for interior trim; the wood is used locally for house sheathing and boxes and is said to be resistant to insect attack on account of its bitterness.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aeschron,* *Ailanthus*,* *Alvaradoa*, *Amaroria*, *Brucea*, *Cadellia*, *Castela*, *Desbordesia*, *Eurycoma*, *Guilfoylia*, *Hannoa*, *Harrisonia*, *Hebonga*, *Holacantha*, *Hyptiandra*, *Irvingella*, *Irvingia*, *Kirkia*, *Klainedoxa*, *Mannia*, *Odyendea*, *Perrieria*, *Picraena*,* *Picramnia*, *Picrasma*,* *Picrella*, *Picrodendron*, *Picrolemma*, *Quassia*,* *Rigiostachys*, *Samadera*, *Simaba*, *Simaruba*, *Simarubopsis*, *Soulamea*, *Spathalea*, *Suriana*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Aeschron, *Ailanthus*, *Alvaradoa*, (*Amaroria*), *Brucea*, (*Cadellia*), *Castela*, (*Desbordesia*), *Dictyoloma*, (*Eurycoma*), *Guilfoylia*, *Hannoa*, (*Harrisonia*), *Holacantha*, *Irvingia*, *Kirkia*, *Klainedoxa*, (*Mannia*), *Odyendea*, *Picramnia*, *Picrasma*, (*Picrodendron*), *Quassia*, *Samadera*, *Simaba*, *Simaruba*, (*Soulamea*), (*Suriana*).

LITERATURE

(i) *On General Anatomy*

Boas 208, Cronquist 503, 504, Davis 551, Engler 642, Jadin 1138, Müller 1572, Pax and Hoffmann 1678, Petaj 1700, Schneider 2043, Spiekerkoetter 2168.

(ii) *On Wood Structure*

de Bastos 147, Benoist 170, den Berger 182, B.H.For.D. 274, Chalk 364, Cooper 461, Greguss 2522, Heimsch 938, Howard 1088, Jaccard 1130, Janssonius 1154, Jentsch 1174, Kanehira 1206, 1209, 1214, Kribs 1283, Lecomte 1334, O'Donnell 1629, Pearson and Brown 1679, Pfeiffer, J. Ph. 1713, Record 1780, 1781, 1783, 1787, 1801, 1809, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Riera 1937, Spiekerkoetter 2168, Stone 2202, 2206, 2207, Tang 2231, Webber 2373, 2374, 2377, 2378, Williams 2430, Yamabayashi 2478.

X 81. BRUNELLIACEAE

(FIG. 77 on p. 334)

SUMMARY

(i) GENERAL

A family of tropical American trees belonging to the single genus *Brunellia*. The young stems are typically 2- or 3-angled at first, and contain a large proportion of **pith**. The most characteristic anatomical characters include the thick-walled, curved, unicellular **hairs**, which often form a felt on the young twigs, and the very striking appearance of the mesophyll of the leaf where, in transverse sections, the palisade and spongy tissues are confined to definite areas between the transcurrent columns of fibres which extend from the vascular bundles to the upper epidermis.

(ii) WOOD

Vessels small, with numerous multiples, perforation plates simple and scalariform, intervacular pitting scalariform and intermediate, pits to ray cells similar. **Parenchyma** absent. **Rays** up to 6 cells wide or exclusively uniseriate, heterogeneous. **Fibres** septate and with simple pits.

LEAF

Dorsiventral. **Hairs**, especially on the lower surface, very thick-walled, unicellular, curved. Cells of the lower **epidermis** densely papillose. **Stomata** not easily observed, but apparently confined to portions of the lower epidermis above the spongy tissue. **Hypoderm**, composed of 1 or 2 layers of thick-walled pitted cells, present beneath the upper epidermis. This tissue is less well developed in *B. comocladifolia* H. et B. than in *B. tomentosa* H. et B. **Mesophyll** composed of about 3 layers of very tall, narrow cells and a relatively smaller region of spongy tissue. Vascular bundles of the **veins** embedded in the spongy mesophyll, but surrounded by sclerenchymatous sheaths, and vertically transcurrent by narrow columns of sclerenchymatous elements extending to the upper epidermis. **Midrib** with a closed but dorsally flattened vascular bundle. **Petiole**, in transverse sections, also exhibiting a closed vascular strand (dorsally concave in *B. tomentosa* but more flattened and interrupted in *B. comocladifolia* (Fig. 77 J)), surrounding a parenchymatous pith, and supported externally by a fairly broad, sinuous ring of thick-walled fibres. A few subsidiary vascular strands also occur in

a latero-superior position. Large solitary and clustered **crystals** sporadically distributed in the palisade tissue, and clustered ones in the parenchymatous tissues of the petiole.

Axis

YOUNG STEM

Cortex containing fairly numerous clustered crystals and stone cells. **Pericycle** with a broad, continuous, somewhat sinuous ring of sclerenchyma, consisting mostly of thick-walled fibres. **Phloem** containing rather infrequent groups of fibres and fairly numerous clustered crystals, the latter smaller than those in the cortex. **Xylem** forming a closed cylinder traversed by uniseriate rays. Vessels in radial groups of 12 or occasionally more (groups rather shorter in *B. comocladifolia* H. et B. than in *B. tomentosa* H. et B.,) seldom exceeding 60 μ in radial diameter; perforations and pitting as described below for the mature secondary xylem. **Pith** large, very heterogeneous, composed of cells with thin but pitted walls. **Crystals**, see 'Cortex' and 'Phloem'.

WOOD

Vessels very to moderately small, mean tangential diameter often less than 50 μ ; solitary and with numerous multiples of 2 to several cells; 5–20 per sq. mm. Perforation plates simple and scalariform. Intervascular pitting scalariform or transitional and, according to Tippon (2261), rarely opposite; pits to ray cells similar, mostly elongated and in scalariform arrangement (1886). Tyloses present. **Parenchyma** absent. **Rays** according to Tippon, 1–6 cells wide; often exclusively uniseriate and more than 12 per mm.; often more than 1 mm. high; heterogeneous (Kribs's Types I and III); with very few procumbent cells when exclusively uniseriate. **Fibres** with pits usually described as simple or indistinctly bordered, e.g. by Record and Hess (1886), but the cells classified as fibre-tracheids by Tippon (2261); septate and with thin walls.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The scalariform perforation plates of the vessels serve to differentiate *Brunellia* from the Simarubaceae, where the genus was included in the Benthams and Hooker system. It is also of interest that the Cunoniaceae, near which the family Brunelliaceae is placed in the respective systems of Engler and Hutchinson, likewise possesses scalariform perforation plates.

(ii) FROM WOOD STRUCTURE

Tippon (2261) makes the following comments on the position of the family. 'The Brunelliaceae are higher than the Hamamelidaceae in the following ways; presence of fibre-tracheids, larger vessel diameter, and presence of some vessel elements with simple perforations. The Brunelliaceae are also higher than the Hydrangeaceae on the basis of these three characters. However, the latter have less oblique vessel end walls, some alternate intervacular pitting, and a higher type of ray in some species.'

GENUS DESCRIBED

(i) FOR GENERAL ANATOMY

The above description is based on specimens of *Brunellia comocladifolia* H. et B.* and *B. tomentosa* H. et B.* in the Kew herbarium.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Brunellia.

LITERATURE

(i) *On General Anatomy*
Engler 637.

(ii) *On Wood Structure*
Bausch 154, Record 1851, Record and Hess 1886, Tippo 2261.

82. CNEORACEAE

(FIG. 76 on p. 330)

SUMMARY

(i) GENERAL

Small shrubs, confined to the Mediterranean region and the Canary Islands. The following description of the leaf and stem, except where stated to the contrary, refers to *Cneorum tricoccum* Linn., grown at Kew.

(ii) WOOD

Vessels mostly in clusters, with radial chains or flame-like clusters in some species, perforations simple, intervacular pitting alternate and minute, pits to parenchyma similar, members extremely short. **Parenchyma** predominantly paratracheal, scanty to aliform, and terminal, sometimes consisting almost entirely of fusiform cells and storied. **Rays** up to 2 or 3 cells wide, with few uniseriats, low and homogeneous in mature material. **Fibres** with simple pits, very short.

LEAF

Dorsiventral. **Hairs** frequently 2-armed and T- or Y-shaped. Multicellular external glands also present. **Epidermis** on both surfaces moderately cutinized, composed of cells with slightly sinuous anticlinal walls. **Stomata** occur sporadically on the upper and abundantly on the lower surface, ranunculaceous, each surrounded by 5 or 6 ordinary epidermal cells. **Mesophyll** consisting of a single layer of palisade cells and a broader, very lacunar, spongy region. Vascular bundles of the smaller **veins** embedded in the mesophyll, each surrounded by a sheath of amyliiferous cells. **Petiole** supplied by an almost completely closed but dorsally flattened vascular strand accompanied by minute, latero-superior, accessory bundles. **Secretory cells**, with oily or resinous contents, present in the mesophyll, but rather inconspicuous unless differentiated by staining.

AXIS

STEM

Cortex mainly parenchymatous, apart from the secretory cells (see below). **Pericycle** containing small, inconspicuous, widely spaced strands of fibres in *C. tricoccum* Linn.; outer part in *C. pulverulentum* Vent. demarcated by an almost continuous ring of sclerenchymatous elements accompanied, according to Engler (640), by cells containing large solitary crystals. **Xylem** and **phloem** forming continuous cylinders traversed by narrow rays. Vessels unevenly distributed, solitary or in irregular clusters, up to about 18 μ in radial diameter, perforations simple. **Pith** consisting of loose parenchyma. **Secretory cells**, with oily or resinous contents, present in the primary cortex, especially in the sub-epidermal region. **Crystals**, see 'Pericycle'.

WOOD (Fig. 76 C-D)

Vessels moderately small (50–100 μ mean tangential diameter) or slightly smaller; commonly in multiples and chains in *Cneorum pulverulentum* Vent. (938), mostly in small multiples and irregular clusters in *C. trimerum* (Urb.) Chodat, and in flame-like clusters in *C. tricoccum* Linn. (938); about 15 per sq. mm. in *C. trimerum*; ring-porous in *C. tricoccum* (938) and sometimes tending to be so in *C. trimerum*; with spiral thickening in *C. tricoccum* (938). Perforations simple. Intervascular pitting alternate and minute; pits to parenchyma typically similar to the intervacular pitting, but, according to Record and Hess (1886), often unilaterally compound. Mean member length about 0.17 mm. **Parenchyma** predominantly paratracheal; scanty in twigs of *C. pulverulentum* and *C. tricoccum* (938), but moderately abundant in mature material of *C. trimerum* (Fig. 76 D), aliform and occasionally linking adjacent vessel groups, with some scattered cells and terminal bands, 1, sometimes 2, cells wide. Consisting in this species almost entirely of fusiform cells, with only occasional strands of 2 cells, and irregularly storied. **Rays** in mature material of *C. trimerum* up to 2, occasionally 3, cells wide, with few and very low uniseriate that are often only 2 cells high; multiseriate rays also very low (less than 10 cells and 250 μ high); about 7 per mm.; homogeneous (Kribs's Type I); tending to be arranged in echelon. The rays of immature twigs, according to Heimsch, higher and heterogeneous. **Fibres** with numerous simple pits on the radial walls. Walls thick. Mean length about 0.7 mm. **Vascular tracheids**, according to Heimsch (938), 'probably occur' in *C. tricoccum*.

TAXONOMIC NOTES

Cneorum was included in the Simarubaceae in the Bentham and Hooker system. Heimsch (938) concludes that, on the basis of wood anatomy, the Cneoraceae are closer to the Rutaceae than to the Zygophyllaceae.

GENUS DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Cneorum.*

* Represented in the Kew slide collection.

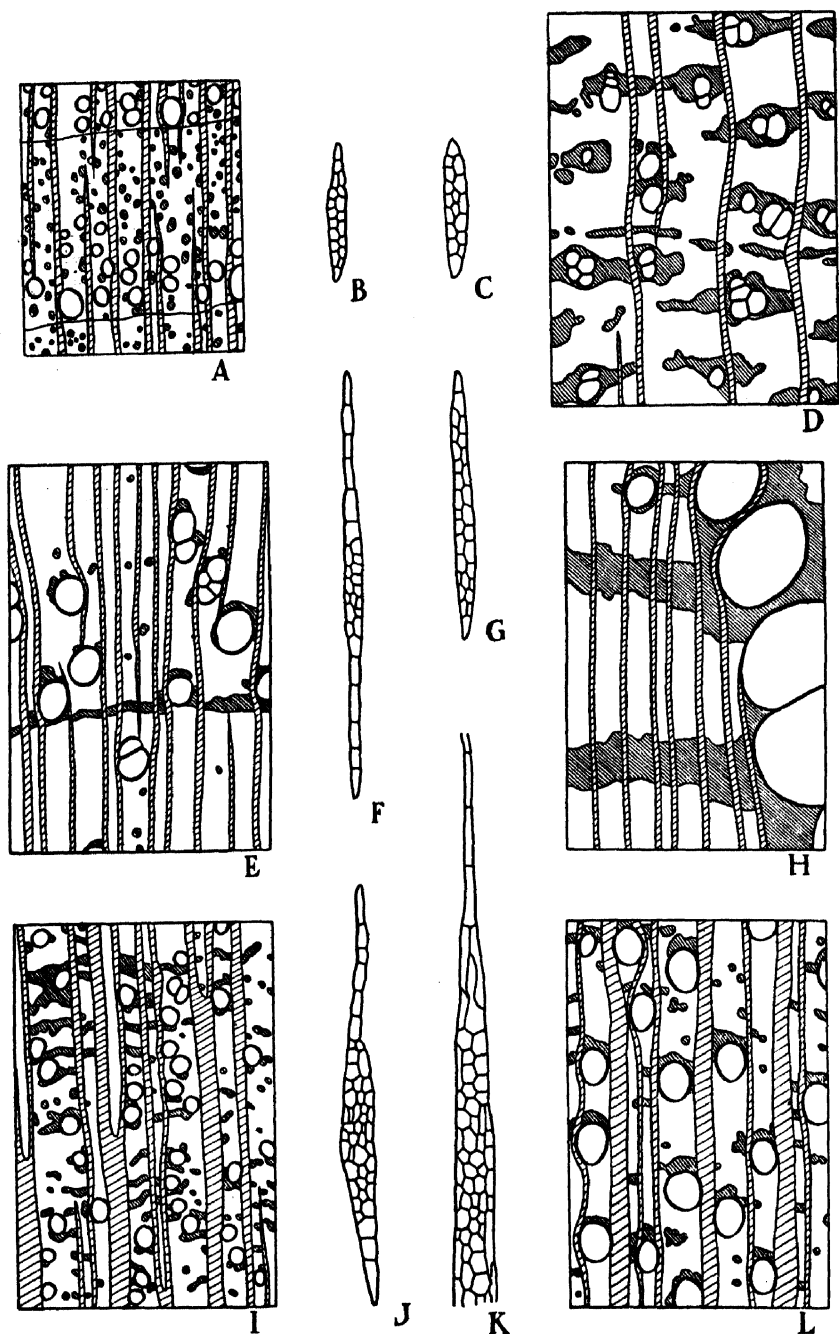


FIG. 76. KOEBERLINIACEAE, A-B; CNEORACEAE, C-D; OCHNACEAE, E-L
 A, *Canotia holacantha* Torr. B, *C. holacantha* Torr. C, *Cneorum trimerum* (Urb.) Chodat. D, *C. trimerum* (Urb.) Chodat. E, *Blastemanthus grandiflorus* Spruce. F, *B. grandiflorus* Spruce. G, *Lophira alata* Banks. H, *L. alata* Banks. I, *Ochna arborea* Burch. J, *O. arborea* Burch. K, *Ouratea amplexans* (Stapf) Engl. L, *Brackenridgea hookeri* (Planch.) A. Gray.

LITERATURE

(i) *On General Anatomy*
Engler 640.

(ii) *On Wood Structure*
Heimsch 938, Record 1783, 1843, 1851, Record and Hess 1886.

✕ 83. KOEBERLINIACEAE

(FIG. 76 on p. 330; FIG. 77 on p. 334)

SUMMARY

(i) GENERAL

This family is represented by the small shrub *Koeberlinia spinosa* Zucc. which forms dense thickets in Texas and Arizona. The tips of the small twigs are differentiated as spines. Minute, deciduous leaves occur. The family also includes the genus *Canotia*.

(ii) WOOD

Vessels very to extremely small, solitary and with spiral thickening in the late wood; ring-porous, intervascular pitting very small and alternate, pits to parenchyma similar; members moderately short. **Parenchyma** apotracheal, as scattered cells or short tangential lines. **Rays** up to 2-7 cells wide, low or high, almost homogeneous, with intercellular canals in *Koeberlinia*. **Fibres** with distinctly bordered pits, sometimes with spiral thickening, very short.

AXIS

YOUNG STEM (The following description applies only to *Koeberlinia spinosa* Zucc.)

Hairs fairly frequent, consisting of short, conical, thick-walled trichomes. **Stomata** situated in deep pits. Outer part of the **primary cortex** differentiated as palisade tissue; inner part parenchymatous and somewhat lacunar. **Cork** arising in the pericycle, consisting of cells with strongly thickened outer tangential walls. **Pericycle** demarcated by large, conspicuous, thick-walled strands of fibres opposite the vascular bundles, connected to form a ring by narrower groups of pitted, lignified cells with comparatively wide lumina. **Phloem** containing isolated or grouped secretory (resin) canals, tangentially compressed in transverse sections of herbarium specimens. **Vascular bundles** separated by relatively broad medullary rays, whose distal ends are slightly enlarged. **Vessels** not very numerous, unevenly distributed, solitary and in irregular clusters, or, less frequently in radial rows, seldom exceeding 15 μ in radial diameter; perforations simple. Wood fibres with thick walls, and slit-shaped, inconspicuously bordered pits. **Pith** composed of slightly lignified parenchymatous cells, many containing solitary crystals which are mostly cubical. A few longitudinal columns of vertically elongated cells with relatively thick walls and granular contents also occur in the pith. **Secretory canals**, see 'Phloem'. **Secretory cells and crystals**, see 'Pith'.

The somewhat similar stem of *Canotia holacantha* Torr. which has narrower rays than *Koeberlinia* is illustrated in Fig. 77 o.

WOOD (Fig. 76 A-B)

Vessels of the late wood very small (25–50 μ mean tangential diameter) to extremely small (less than 25 μ); solitary; very numerous in *Canotia* (200 per sq. mm.); often ring-porous; spiral thickening present in the late wood vessels of stemwood of *Canotia* and *Koeberlinia* but absent from the pore-zone vessels; present in all vessels of branchwood of *Koeberlinia* (1806). Intervascular pitting alternate, minute; pits to ray and wood parenchyma cells similar to the intervascular pitting. Dark deposits common in *Koeberlinia* (1806). Mean member length 0.3 mm. **Parenchyma** apotracheal, as scattered cells or short tangential lines. Strands usually of 4 cells. **Rays** up to 7 cells wide and high in *Koeberlinia* (1886), up to 2 cells wide, low and about 14 per mm. in *Canotia*; uniseriate numerous in *Canotia*, often only 1 or 2 cells high, composed almost entirely of procumbent cells; almost homogeneous (Kribs's Type I); with numerous solitary crystals in *Canotia*. Record (1806) notes the presence in *Koeberlinia* of 'numerous radial intercellular canals, varying in size from a pin-hole to a lenticular cavity one-sixteenth inch high, observed in larger stems but not in small ones. They resemble those found in certain Apocynaceae and Euphorbiaceae.' **Fibres** with distinctly bordered pits on both radial and tangential walls; walls thick; spiral thickening sometimes present but not very distinct. Mean length about 0.5 mm. A tendency to ripple marks has been noted (1886) in one specimen of *Koeberlinia*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Koeberlinia differs from the Simarubaceae, amongst which it was included in the system of Bentham and Hooker, in having pericyclic cork, and widely separated vascular bundles. It resembles many of the Simarubaceae, on the other hand, in possessing secretory canals, but whereas those of the Simarubaceae commonly occur in the pith, those of *Koeberlinia* are present in the phloem. These facts seem to justify the exclusion of *Koeberlinia* from the Simarubaceae.

GENUS DESCRIBED

(i) FOR GENERAL ANATOMY

Koeberlinia.* The description is based mainly on an examination of material from the Kew herbarium.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Canotia, (*Koeberlinia*).

LITERATURE

On Wood Structure

Record 1806, 1851, 1864–6, Record and Hess 1886.

✓ 84. OCHNACEAE

(FIG. 76 on p. 330; FIG. 77 on p. 334)

SUMMARY

(i) GENERAL ANATOMY

A tropical family of trees, shrubs, or very rarely herbs. **Hairs** are infrequent, but unicellular, uniseriate, or multicellular when present. The **leaf** is usually dorsiventral. **Stomata** in the leaf are usually but not invariably confined to the lower surface, and are sometimes rubiaceous. Cells with strongly thickened inner tangential and radial walls, the lumen of each cell being completely filled with a large clustered, or, more rarely, a solitary crystal, occur in the parenchymatous tissues, especially in *Brackenridgea*, *Elvasia*, *Ochna*, and *Ouratea*. These elements, termed '**cristarque cells**' (Fig. 77 F), are most frequent in the outer or inner part of the cortex of the petiole and young stem, as well as in the region of the lateral veins of the leaf. Those in the young stem and petiole are often arranged in a continuous or interrupted layer just below the epidermis. Various orientated medullary bundles have been recorded in the **petiole** of *Blastemanthus*, *Cespedesia*, *Godoya*, *Hilairella*, *Planchonella*, and *Poecilandra*; and similar **medullary bundles** of various types in the pith of the stem of *Cespedesia*, *Godoya*, and *Planchonella*. **Cortical bundles** are nearly always present in the stem. The **cork** is superficial in origin, sometimes arising in the epidermis itself, and is composed of thin-walled cells or of cells with thickened tangential walls. The **pericycle** of the stem nearly always contains isolated groups of fibres. The **xylem** and **phloem** of the young stem are usually in the form of continuous cylinders traversed by narrow rays.

(ii) WOOD

Vessels sometimes almost exclusively solitary, occasionally with some radial pattern, perforations typically simple, intervacular pitting alternate, very small to minute, pits to ray cells similar; with vested pits in the Exalbuminosae; members of medium length. **Parenchyma** typically paratracheal and often scanty in the Albuminosae of Gilg, apotracheal (abundant diffuse) in the Exalbuminosae, though with a tendency towards abaxial aliform types; in broad bands in *Lophira*. **Rays** up to 2-8 cells wide, often high; markedly heterogeneous, except in *Lophira*. **Fibres** with simple to distinctly bordered pits; of medium length to moderately long.

LEAF

Generally dorsiventral, but occasionally centric in certain species of *Ouratea*. **Hairs** infrequent; unicellular, uniseriate, or multicellular when present. Glandular shaggy hairs recorded on the stipules of *Godoya* and on the leaf teeth of *Lavrada glandulosa* St. Hil. Cuticle on the upper epidermis stated by Beauvisage (163) to be thick in *Strasburgeria*. **Epidermis** composed of cells with straight anticlinal walls in *Blastemanthus* and *Luxemburgia*, with sinuous walls in *Ochna*; inner walls often mucilaginous and sometimes penetrating into the mesophyll in *Brackenridgea*, *Elvasia*, *Hilairella*, *Luxemburgia*, *Ochna*, and *Ouratea*; sometimes papillose. Epidermal cells specially large and serving for water storage in *Sauvagesia racemosa* St. Hil. **Stomata**

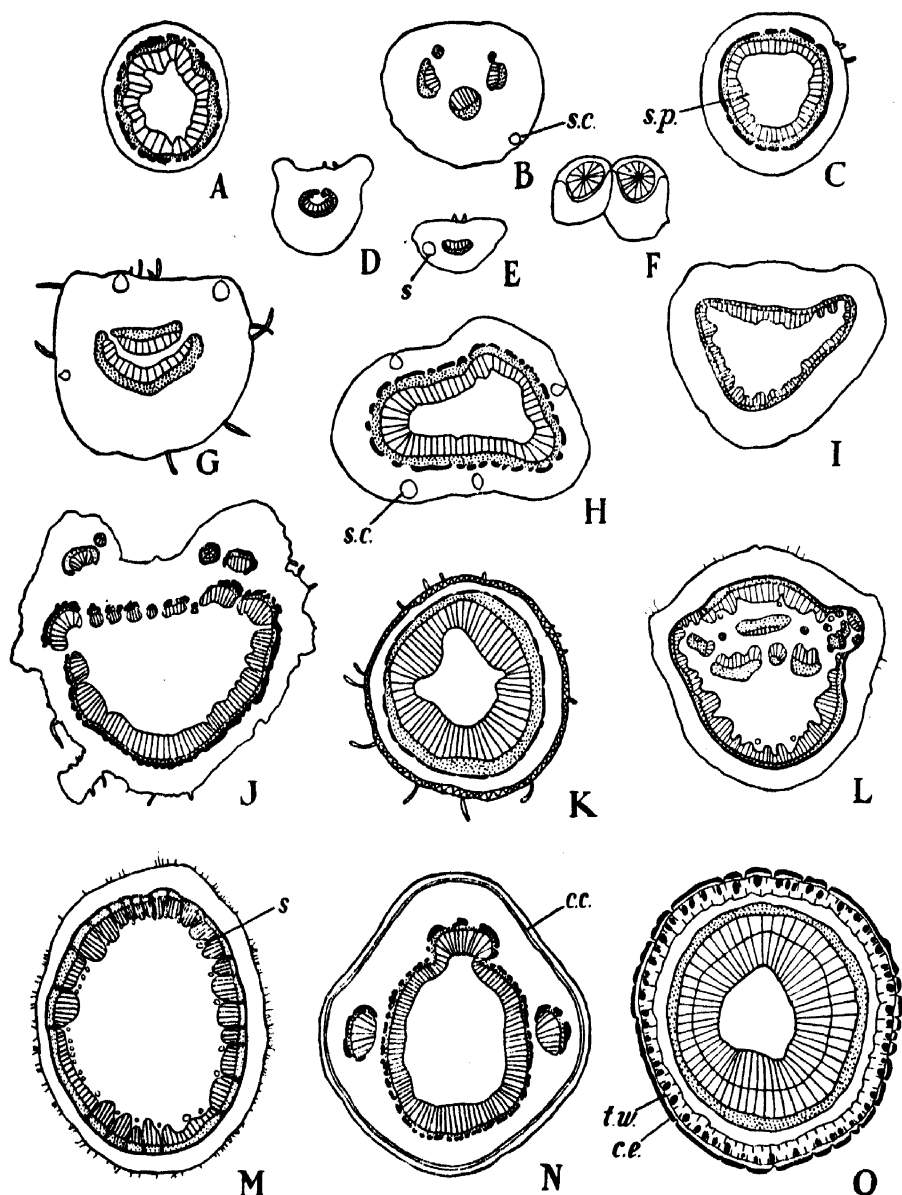


FIG. 77. MELIACEAE, A and D; RUTACEAE, B, E, and G-H; OXALIDACEAE, C and K; OCHNACEAE, F and N; SIMARUBACEAE, I and L-M; BRUNELLIACEAE, J; KOEBERLINIACEAE, O

A, *Khaya senegalensis* A. Juss. Petiole $\times 12$. B, *Ruta graveolens* Linn. Petiole $\times 15$. C, *Averrhoa carambola* Linn. Petiole $\times 15$. D, *Turraea obtusifolia* Hochst. Petiole $\times 15$. E, *Barosma betulina* Bartl. et Wendl. Petiole $\times 15$. F, *Gomphia* sp. Cratarque cells $\times 283$. G, *Choisya ternata* H. B. et K. Petiole $\times 15$. H, *Citrus aurantium* Linn. Young stem $\times 15$. I, *Aeschrion excelsa* (Sw.) Kuntze. Petiole $\times 11$. J, *Brunellia comocladifolia* Humb. et Bonpl. Petiole $\times 9$. K, *Averrhoa carambola* Linn. Young stem $\times 15$. L, *Ailanthus altissima* Swingle. Petiole $\times 11$. M, *A. altissima* Swingle. Young stem $\times 8$. N, *Gomphia* sp. Young stem $\times 15$. O, *Canotia holacantha* Torr. Stem $\times 12$.

c.c. Layer of cratarque cells. c.e. Cutinized epidermis. s. Secretory canals. s.c. Secretory cavity. s.p. Spongy pith. t.w. Zone of small cells with thin walls.

often but not invariably confined to the lower surface, sometimes rubiaceous, but subsidiary cells reported to be absent from *Lophira* and *Strasburgeria*. Stomata arranged in crowded groups between the network of veins in *Godoya*. **Hypoderm** present beneath the upper epidermis in *Strasburgeria* (consisting of mucilaginous cells) and *Lophira*. 'Spicular cells' (sclerenchymatous idoblasts) form a continuous layer below the upper epidermis in *Blastemanthus*, *Cespedesia*, *Elvasia*, *Hilarella*, *Luxemburgia*, *Poecilandra*, *Trichovaselina*, *Vaselina*. Similar cells sometimes accompany the vascular bundles of the veins and have branches extending into the mesophyll. **Mesophyll** including a single layer of palisade tissue in *Brackenridgea*, *Elvasia*, *Ochna*, and *Ouratea*, and large mucilage cells in *Euthemis* and *Strasburgeria*. Vascular bundles of the lateral **veins** accompanied by abundant sclerenchyma, the smaller ones often vertically transcurrent. Separate bundles enter the base of, but generally unite within, the **petiole** to form a closed or slightly dissected ring, although the vascular strand sometimes remains open in *Elvasia* and *Ouratea* or crescent-shaped as in *Ochna atropurpurea* DC. Various orientated medullary bundles recorded in the petiole of *Blastemanthus*, *Cespedesia*, *Elvasia*, *Godoya*, *Hilarella*, *Planchonella*, *Poecilandra*, *Trichovaselina*, *Vaselina*. Petiole of *Wallacea* containing a ring of bundles surrounding 2 medullary strands, one of the latter normally and the other inversely orientated, together with centric cortical bundles consisting of a central mass of xylem surrounded by phloem fibres. Petiole of *Strasburgeria* with 5 vascular strands at the base, but the median central and 2 adjoining lateral ones appear as 2 rings in transverse sections through the distal end, the 2 remaining laterals being closed or sometimes U-shaped according to Beauvisage (163). Isolated bundles present in the petiole of *Lophira*. 'Cristarque cells' frequent below the epidermis of the petiole in *Brackenridgea*, *Elvasia*, *Gomphia*, *Ochna*, and *Ouratea*, sometimes occurring in the endodermal region or outer cortex as well. **Crystals** mostly clustered but frequently solitary, generally accompanying the vascular bundles of the veins, but also in *Sauvagesia* scattered in the mesophyll; sometimes situated in so-called 'cristarque cells' with U-shaped thickenings to the walls. The 'cristarque cells' accompany the vascular bundles in *Brackenridgea*, *Elvasia*, *Ochna*, and *Ouratea*. (See also under 'Petiole'). Crystals said to be absent from *Lavradia* spp.

AXIS

YOUNG STEM (Fig. 77 N)

Cork superficial in origin, sometimes arising in the epidermis itself in *Ochna* and *Ouratea*. **Cortex** containing 'cristarque cells' (Fig. 77 F) (see also 'Summary' and 'Leaf') in *Brackenridgea*, *Elvasia*, *Gomphia*, *Ochna*, *Ouratea*, most frequently situated below the epidermis, but also occurring in the region of the endodermis as well as in the central tissues of the cortex. The mode of differentiation and distribution of the 'cristarque cells' is stated by Solereder to be of specific diagnostic value. **Cortical vascular bundles**, consisting of the bases of the lateral vascular strands to the leaves which branch off from the conducting system of the stem in the region below the nodes, occur throughout the family, but their number and size are variable. Twenty-four or more cortical bundles are present in *Lophira*, whilst they are also well developed and numerous in *Lavradia* and *Schuermansia*, but less frequent in

Leitgebia and *Sauvagesia*. Bases of the internodes sometimes devoid of cortical bundles. Cortex also including stone cells as well as abundant clustered and/or solitary crystals in most of the genera including *Lophira*. **Pericycle** nearly always containing strands of fibres, but sometimes with a continuous or almost continuous ring of sclerenchyma in *Ouratea* owing to the cells between the fibre bundles becoming sclerosed. Pericycle in *Lophira* and *Strasburgeria* at first containing isolated strands of fibres, but these unite subsequently to form a continuous ring. **Xylem** and **phloem** usually constituting closed cylinders. Secondary phloem sometimes containing fibres; stratified into hard and soft portions in *Godoya*, the structure as seen in transverse section in this genus recalling that of *Tilia*. Vessels mostly scattered in *Ochna* and *Ouratea*; radially arranged in *Luxemburgia*; perforations usually simple, and circular or elliptical; but in some genera, including *Lavradia* and *Sauvagesia*, accompanied by scalariform plates with a few bars, or with a larger number of bars in *Luxemburgia*. Scalariform perforation plates also recorded by Beauvisage (163) in *Strasburgeria*. **Pith** often becoming lignified at an early stage; sometimes containing **medullary bundles**, the latter consisting of vessels and fibrous cells in *Godoya* and *Planchonella*, but of phloem and fibrous cells in *Cespedesia*. Medullary bundles assume a more normal structure in the axis of the inflorescence. Bundles of fibres occur in the pith of *Lophira*, where some are divided into chambers, each containing a solitary crystal. Medullary bundles stated to be absent from the axis in *Blastemanthus*, *Hilairella*, *Luxemburgia*, and *Poecilandra*, although occurring in the petiole of some of these genera (see 'Leaf'). **Crystals**, see 'Cristarque cells', 'Cortex', and 'Pith'. **Mucilage sacs** or **passages** present in the cortex and pith of *Euthemis*, *Sauvagesia*, *Schuermansia*, and *Strasburgeria*. Irregularly distributed **secretory cells**, containing granular or refractive, probably tanniniferous material which is stained readily by safranin, occur in the cortex, phloem, ray cells, and pith of *Gomphia* sp. and *Ochna atropurpurea* DC. and probably in other unexamined genera and species as well.

WOOD (Fig. 76 E-L)

Vessels mostly small (mean tangential diameter less than $100\ \mu$), sometimes very small ($25\text{--}50\ \mu$), medium-sized in *Blastemanthus* (1886), *Cespedesia*, and *Wallacea* and moderately large in *Lophira*; almost exclusively solitary in *Brackenridgea*, *Elvasia* p.p., *Ochna*, and *Ouratea*, with multiples of 2-3 cells moderately common in the other genera, with a loose oblique pattern in *Lophira*; according to Solereder, with a radial arrangement in *Luxemburgia*; very variable in number, ranging from about 2 per sq. mm. in *Cespedesia* and *Lophira* to 80-150 per sq. mm. in *Ochna arborea* Burch. (360), mostly between 20 and 50 per sq. mm. Perforations exclusively simple except in *Lavradia*, *Luxemburgia*, and *Sauvagesia*, for which Solereder records some scalariform plates. Intervascular pitting alternate, very small to minute; pits to ray cells similar. Vested pits reported by Bailey (78) in 5 genera of the Exalbuminosae. Tyloses observed only in a single specimen of *Blastemanthus grandiflorus* Spruce; solid deposits present in *Blastemanthus*, *Lophira*, and *Ochna*. Mean length 0.5-0.9 mm. **Parenchyma** (a) paratracheal, in *Blastemanthus* (Fig. 76 E), *Cespedesia*, *Tyleria*, and *Wallacea*, typically scanty and confined to a few cells round the vessels, but more abundant and irregularly vasicentric

in *Cespedesia macrophylla* Benth.; (b) predominantly apotracheal in *Brackenridgea*, *Elvasia*, *Ochna* (Fig. 76 I), and *Ouratea*, typically diffuse and in short uniseriate lines (sometimes wider in *Elvasia*) that often tend to be associated with the abaxial sides of the vessels, e.g. in *Brackenridgea hookeri* A. Gray (Fig. 76 L), *Elvasia essequiboensis* Engl., and some species of *Ouratea*, e.g. *O. amplexans* Hutch. et Dalz. and that formerly known as *Gomphia oblongifolia* Ridl.;¹ and (c) as regular, broad, continuous bands 3–4 cells wide in *Lophira* (Fig. 76 H). Distinct terminal bands observed only in *Blastemanthus* and *Tyleria*. Crystals in chambered cells present in small numbers in *Cespedesia* and *Elvasia*, abundant in *Lophira*; dark-coloured gum abundant in all the species examined. Strands commonly of 8 or more cells. **Rays** multiseriate, 2–3 cells wide in *Blastemanthus*, *Elvasia* p.p., *Lophira*, and *Wallacea*, 4–8 cells wide in the remainder; commonly 1 mm. or more in height except in *Lophira*; uniseriates typically numerous and composed entirely of high upright cells, but with both square and upright cells in *Blastemanthus grandiflorus* Spruce; uniseriates often rather few in *Lophira* and composed entirely of procumbent cells; 10–20 per mm., most numerous in *Blastemanthus* and fewest in *Lophira*; homogeneous (Kribs's Type I) in *Lophira* but markedly heterogeneous (Kribs's Type I) in the other genera, commonly with 10 or more rows of upright or square marginal cells; sheath cells present in *Brackenridgea*, *Ochna*, and *Ouratea*. Single crystals occasionally present in the ordinary cells; large thick-walled idioblasts, each containing a single crystal present in *Ochna* and *Ouratea* (except *Ouratea oblongifolia*); similar, but smaller, cells occur in *Elvasia*; cells containing abundant, dark-coloured gum. The multiseriate rays, except in *Blastemanthus* and *Lophira*, appear to be derived from the splitting of very high primary rays; very high rays (up to about 8 mm.) occur sporadically and the rays tend to be of 2 distinct sizes. **Fibres** with simple pits in *Tyleria* and *Wallacea*, with small to moderately distinct bordered pits in the other genera; pits usually rather more numerous on the radial than on the tangential walls; pits numerous in *Elvasia*, *Ochna*, and *Ouratea*; some fibres septate in *Tyleria*. Walls very thick, the secondary wall often showing distinct zones. Mean length 1.2–2.0 mm. **Vascentric tracheids** present in small numbers in *Lophira*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The only outstanding characteristic for the whole family is the possession of cortical bundles. These occur not only in the genera whose inclusion in the family has been long established but also in *Lophira* which was treated in the Bentham and Hooker system as belonging to the Dipterocarpaceae and in *Lavradia*, *Leitgebia*, *Sauvagesia*, and *Schuermansia* which the same authors included in the Violaceae. The presence of 'cristarque cells' in *Brackenridgea*, *Elvasia*, *Gomphia*, *Ochna*, and *Ouratea* is an important feature which confirms the existence of close affinities between these genera, but serves to differentiate them from other genera in the family in which these special cells have apparently not been recorded. The presence of mucilage cells and

¹ This species is now considered to be an *Ouratea*, but the specific epithet has already been used for *Ouratea oblongifolia* Rusby and no new combination appears to have been published.

passages in *Euthemis*, *Sauvagesia*, *Schuurmansia*, and *Strasburgeria* serves to distinguish these genera rather clearly from the others.

(ii) FROM WOOD STRUCTURE

The genus *Lophira* differs from all the others, particularly in its parenchyma and its much more highly specialized rays. Such affinities as it has with the family would appear to be with the Exalbuminosae, possibly through *Elvasia*, rather than with the Albuminosae. Vestal (2329) suggests that there may be a connexion between the Ochnaceae and the Dipterocarpaceae through *Lophira*.

Gilg's two sub-families Exalbuminosae and Albuminosae are clearly distinguishable in their wood structure by the nature of the parenchyma and the presence of vested pits in the Exalbuminosae. Vestal also notes a greater elongation of the upright cells in the rays as characteristic of the Albuminosae, but this does not appear to be entirely dependable.

Illustrations of the wood of *Testulea gabonensis* Pellegr. given by Normand (1612) show a general resemblance to the Ochnaceae in the cross-section, but a much more highly specialized ray type, comparable with that of *Lophira*.

ECONOMIC USES

The only timber of commercial importance is Ekki, the product of *Lophira alata* var. *procera* Burt Davy. This is a very hard, durable wood, used chiefly for sleepers and marine piling. The wood of *Ochna arborea* Burch. is used in South Africa for the handles of tools. Meni oil is obtained from the seeds of *Lophira alata* Banks.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Blastemanthus, Brackenridgea, Cespedesia, Elvasia, Euthemis, Godoya, Gomphia,* Hilairella, Lavradia, Leitgebia, Lophira, Luxemburgia, Ochna,* Ouratea, Planchonella, Poecilandra, Sauvagesia, Schuurmansia, Strasburgeria, Trichovaselina, Vaselia, Wallacea.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Blastemanthus, Brackenridgea, Cespedesia, Elvasia, (Lavradia), Lophira, (Luxemburgia), Ochna, Ouratea, (Sauvagesia), Tyleria, Wallacea.

LITERATURE

(i) On General Anatomy

Beauvisage 163, Gilg 770, Privault 1759.

(ii) On Wood Structure

Bailey 78, Bausch 154, Besson 186, Chalk 360, 364, Cooper 461, Foxworthy 705, Hopkinson 1083, Jentsch 1173, Lecomte 1335, Méniaud 1491, Normand 1612, Record 1843, 1851, Record and Hess 1886, Record and Mell 1894, Riera 1937, Stone 2206, Thieme 2247, Vestal 2329, Williams 2430.

85. TETRAMERISTACEAE

(FIG. 79 on p. 346)

SUMMARY

(i) GENERAL

The family is represented by the sole genus *Tetramerista* which includes a few arboreal species in the Malayan region. The most interesting anatomical character is the occurrence of **raphides**.

(ii) WOOD

Vessels large and mostly in multiples of 2-4 cells, perforations simple, intervacular pitting alternate and minute, pits to ray cells similar, members very long. **Parenchyma** apotracheal, diffuse. **Rays** up to 4-5 cells wide, very high, markedly heterogeneous; with raphides in enlarged cells. **Fibres** with simple pits and very thin walls, very long.

LEAF

Dorsiventral. **Hairs**. None observed. **Epidermis** on both surfaces composed of pentagonal and hexagonal, moderately thick-walled cells, covered externally with a striated cuticle. **Stomata** confined to the lower surface; each surrounded by 4, or sometimes more, ordinary epidermal cells (ranunculaceous), 2 of which are parallel to the pore in some instances (rubiaceous). A single layer of **hypoderm** with pitted cell walls occurs beneath the upper epidermis. **Mesophyll** composed of 1 or 2 rows of palisade cells and a much broader region of spongy tissue. Vascular bundles of the smaller **veins** embedded in the mesophyll, partly surrounded by thick-walled fibres. **Midrib** and leaf base supplied by a solitary, annular vascular strand which is flattened or slightly concave towards the adaxial surface, and supported at the periphery by a continuous ring of moderately thick-walled fibres. A few sclerenchymatous idioblasts occur in the midrib and also in the central part of the mesophyll. **Crystals**. Large cells containing raphides or crystal-sand present in the midrib and in the palisade layer of the mesophyll.

AXIS

YOUNG STEM

Cork arising in the inner part of the cortex. **Cortex** containing scattered stone cells, either isolated or in groups. **Pericycle** not well defined in the material available. **Phloem** and **xylem** in the form of continuous cylinders traversed by narrow rays. Scattered stone cells similar to those in the cortex, also present in the phloem. Vessels mostly in radial rows, somewhat angular, seldom exceeding 60 μ in radial diameter; perforations mostly simple, very oblique, but others with scalariform plates with about 8 thin bars. Wood fibres with narrowly bordered pits with elongated, slit-shaped apertures. **Pith** composed of moderately thick-walled, pitted cells. **Crystals**. Raphides occur in special cells in the pith and phloem, similar cells filled with crystal-sand also being present in the phloem.

WOOD (Fig. 79 H-I)

Vessels large (mean tangential diameter more than $200\ \mu$); solitary and in numerous multiples of 2-4 cells; about 2-3 per mm. Perforations simple, moderately oblique. Intervascular pitting alternate, minute; pits to ray and wood parenchyma cells similar. Mean length about 1.5 mm. **Parenchyma** apotracheal, typically as scattered cells, but with a tendency to continuous bands in some specimens. Strands usually of 8 cells. **Rays** up to 4-5 cells wide and often several millimetres high; uniseriates moderately numerous and composed of square and upright cells, but largely replaced in some specimens by the marginal rows of the multiseriate rays; about 10 rays per mm.; markedly heterogeneous (Kribs's Type I), with up to 10 to very many marginal rows of square to upright cells, these cells often biseriate near the procumbent cells. Enlarged procumbent cells containing raphides present in the multiseriate rays. **Fibres** with simple pits that occur mainly in the radial walls. Walls very thick. Mean length about 2.5 mm.

TAXONOMIC NOTES

The taxonomic position of *Tetramerista* is not well established. It differs from the Ochnaceae in lacking cortical bundles in the young stem, and from the Theaceae in possessing raphides. On the advice of Dr. J. Hutchinson it is here treated as a separate family.

The wood anatomy generally does not support the inclusion of *Tetramerista* in either the Ochnaceae or the Marcgraviaceae, though the occurrence of raphides in the rays of both *Tetramerista* and *Marcgravia* may indicate some affinity with the last genus. The wood of *Tetramerista* shows a greater general resemblance to that found in the Theaceae, but the genus stands out as exceptional if included in this family. The evidence of wood anatomy supports Dr. Hutchinson's advice to treat *Tetramerista* as a distinct family.

Although, as already stated, *Tetramerista* has some features in common with the Marcgraviaceae, it does not agree very closely with any one genus. For example, while it has the raphides of *Marcgravia* and *Souroubea*, its vessel groups, non-septate fibres, and diffuse parenchyma link it with *Norantea* rather than *Marcgravia*; it differs from all three genera in having minute intervacular pitting.

Vestal (2329) states that in its minute wood anatomy *Tetramerista* 'resembles in all characters the Caryocaraceae, except in ray type and the presence of crystals in the genus *Caryocar*'; but in the material examined by the author the resemblance is less marked, particularly as regards type of intervacular and vessel-ray pitting; the parenchyma, too, may differ considerably and the occurrence of raphides in the rays of *Tetramerista* is a further point of difference.

ECONOMIC USES

The timber, according to Desch (574), is of local importance in Malaya and has been commonly obtainable in the Singapore market from the adjacent Dutch islands.

GENUS DESCRIBED

(i) FOR GENERAL ANATOMY

Tetramerista.* The material examined was *T. glabra* Miq. from the Kew herbarium.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Tetramerista.

LITERATURE

On Wood Structure

Desch 574, Hess 959, Vestal 2329.

86. BURSERACEAE

(FIG. 78 on p. 342; FIG. 79 on p. 346)

SUMMARY

(i) GENERAL

A tropical family of resinous trees and shrubs. The **hairs** are of various types and include simple and stellate clothing trichomes, as well as glandular hairs which may be either capitate or snail-shaped. The **epidermis**, particularly on the upper surface of the leaf, often contains a proportion of mucilage cells. Similar cells also occur, although more rarely, in the mesophyll or in the parenchymatous tissues of the stem. **Stomata** sometimes occur on both surfaces of the leaf but are more frequently confined to and always more numerous on the lower side; they are ranunculaceous. **Hypoderm**, on the upper side of the leaf, is infrequent and limited to a few genera. In the **mesophyll** the palisade tissue most frequently consists of a single layer, but exceptions occur. The **petiole** is usually cylindrical or dorsally flattened, sometimes winged, and, in transverse sections, nearly always exhibits a complete circle of vascular bundles, whilst medullary bundles are enclosed within the circle in *Canariellum*, *Canarium*, *Dacryodes*, *Pachylobus*, *Santiria*, and *Trattinickia*. **Cork** generally arises in the sub-epidermis of the young stem, whilst the **cortex** sometimes contains sclerenchymatous idioblasts. The **pericycle** is characterized either by arcs or a composite continuous ring of sclerenchyma. The **xylem** and **phloem** constitute closed cylinders traversed by medullary rays 1-2 cells wide. The phloem often includes a proportion of fibres. The **pith** of the stem may be homogeneous or heterogeneous, usually lignified. Inversely orientated **medullary bundles** occur in the stem of all species of *Canarium*. **Secretory canals** generally present in the phloem of both leaf and stem, and occur in the pith as well in a few species. For **mucilage cells** see 'Epidermis'. Solitary and clustered **crystals** are frequent, e.g. in the cortex.

Whilst the Burseraceae as a whole are fairly well defined anatomically, the component genera cannot easily be distinguished. The genus *Protium* for instance is anatomically homogeneous, but in *Commiphora* the range of structure amongst different species is almost as wide as in the whole of the family. A considerable range of variation occurs also in *Bursera*.

(ii) WOOD

Vessels moderately small to medium-sized; perforations exclusively simple, intervacular pitting alternate, with large hexagonal borders, pits to ray cells and parenchyma large, simple and unilaterally compound; members of medium length. **Parenchyma** paratracheal; varying from scanty to vasicentric and occasionally with some diffuse. **Rays** up to 2-4 cells wide with few uniseriats; heterogeneous; enlarged cells containing single crystals present in some species; in echelon or storied locally in some genera. **Fibres** septate; with small simple pits; of medium length to moderately long. **Inter-cellular canals** present in the rays of many species.

LEAF

Generally dorsiventral; occasionally isobilateral. **Hairs** include the following diverse kinds. (i) Simple, sometimes either hooked or 2-armed. (ii) Stellate

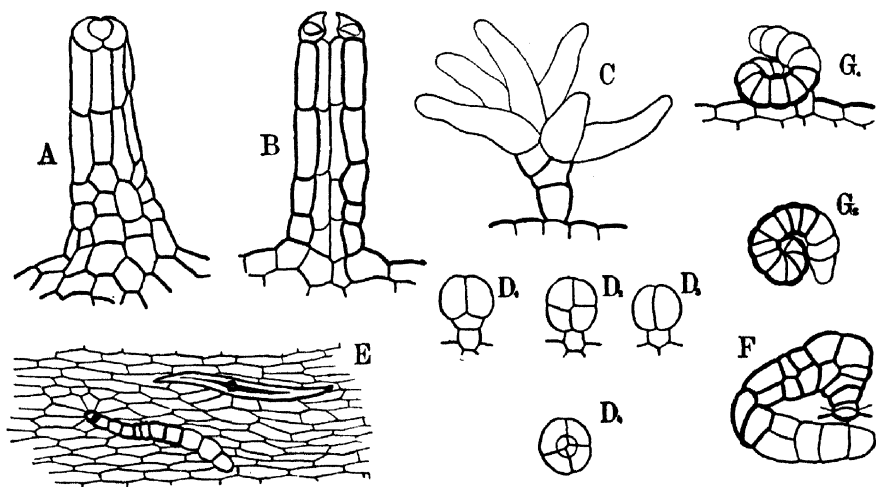


FIG. 78. BURSERACEAE

A-B, Elevated stomata of *Santiria mollis* Engl. C, Branched trichome of *Santiria mollis*. D-G, External glands: D, *Boswellia papyrifera* (Delile) A. Rich.; E, *Protium spruceanum* (Benth.) Engl.; F, *Canarium hispidum* Bl.; G, *Crepidospermum rhoifolium*, Tr. et Planch.—By Solereder.

and tufted, e.g. in species of *Canarium* and *Santiria* (Fig. 78 c). (iii) Glandular, either capitate or snail-shaped. Glandular hairs with stalks of 1-2 cells and 2- to 4-celled heads recorded in *Boswellia papyrifera* (Delile) A. Rich. (Fig. 78 D), similar hairs with rather longer stalks in *Canarium acutum* Engl. and *Garuga pinnata* Roxb., thread-like hairs broadened at the apex in *Protium spruceanum* (Benth.) Engl. (Fig. 78 E). Snail-like glands reported by Solereder in species of *Canarium* (Fig. 78 F), *Crepidospermum* (Fig. 78 G), *Pachylobus*, *Santiria*. These various kinds occur either alone or together and their distribution is of specific diagnostic value. Lower surface of the lamina provided with open grooves filled with small hairs in *Trattinickia rhoifolia* Willd. **Epidermis** somewhat variable in structure, frequently including a varying proportion of mucilage cells. Mucilaginous cells recorded in the upper epidermis of *Bursera angustata* Griseb., *B. aptera* Ramir, *B. bipinnata* (Schlecht) Engl. (whole

epidermis), *B. multijuga* Engl. (scattered), *Canarium boivini* Engl., *Commiphora* spp. *Pachylobus* spp., *Protium* spp. Mucilage cells present on the lower side in *Bursera aptera* and rarely in *Pachylobus*; absent from *Tetragastris*. Lower epidermis papillose in *Canariellum*, *Commiphora* spp. (papillae described as external idioblasts), and *Trattinickia* sp.; containing groups of silicified cells in *Protium*. **Stomata** present on both surfaces or limited to, and always more numerous on, the lower side; ranunculaceous. Stomata recorded on both surfaces in certain species of *Commiphora* and *Tetragastris*; confined to the lower surface in other species of *Commiphora*; situated at the tips of columnar elevations above the network of veins in *Santiria mollis* Engl. (Fig. 78 A-B). **Hypoderm** recorded below the upper epidermis in *Aucoumea* (cells elongated and thickened), *Canariellum* (2 or 3 layers), certain species of *Commiphora*, *Dacryodes*, and *Triomma*. **Mesophyll** generally dorsiventral, but palisade tissue recorded beneath both surfaces in a few species, notably in *Commiphora*. Palisade tissue consisting of 1 layer in *Canarium* (sometimes double in the section *Monodelpha* Engl.), *Commiphora*, *Crepidosperrum* (pro parte), *Dacryodes*, *Garuga*, *Pachylobus* (usually), *Protium* (very rarely 2 layers), *Tetragastris*, *Trattinickia*, *Triomma*; consisting of more than 1 layer in *Aucoumea*, *Boswellia*, *Canariellum*, *Crepidosperrum* (pro parte), *Pachylobus* (sometimes) and *Santiria*. Some of the palisade cells mucilaginous in *Canarium*, *Protium*, *Santiria*, and *Trattinickia*, those of *Protium* occasionally contain a crystal as well. Crystalliferous cells also occur in the palisade layer of *Scutinanthe*. Mesophyll exhibiting a considerable range of structure in different species of *Trattinickia*; containing mucilage cells in certain species of *Commiphora*. Spongy mesophyll well developed, in the particularly thick lamina of *Canariellum*. Vascular bundles of the small **veins** containing secretory canals in the pith in *Canarium*, and in the phloem of the larger veins in most genera. Bundles vertically transcurrent in *Dacryodes* and *Protium*. **Petiole**, in transverse sections, nearly always exhibiting a circle of vascular bundles, e.g. in *Canariellum*, *Canarium*, *Pachylobus*, *Santiria*, *Trattinickia*, the outer ring enclosing medullary bundles, often inversely orientated, in *Canariellum*, *Canarium*, *Dacryodes*, *Pachylobus* (excluding *Sorindeia juglandifolia* Oliv. var. *dahomensis* A. Chev. (syn. *P. dahomensis* Engl.), and *Santiria*. Petiolar bundles normally in a circle, but occasionally in arcs in *Commiphora*. Petiole of '*Scutinanthe boerlagii* Hochr.' containing a ring of xylem and phloem surrounding a central, normally orientated mass of xylem and phloem. Petiole of *Bursera* very variable in transverse sections through the distal end, with a ring of xylem and phloem supported by a closed ring of sclerenchyma in *B. tonkinensis* Guill.; with an arc of 4 bundles and 2 lateral masses of collenchyma in *B. galeottiana* Engl.; with an open arc of bundles surrounded by a collenchymatous sheath in *B. aptera*. A layer of cork has been recorded on one side of the petiole in *Tetragastris*. 'Cortex' of the petiole containing numerous sclerenchymatous idioblasts in *Canariellum* and a smaller number in *Dacryodes*, and very numerous crystals in *Commiphora*. **Petiolules** provided with basal swellings, believed to have a motor function, in *Aucoumea*, *Canarium*, and *Pachylobus*. **Crystals**, see 'Mesophyll'. **Secretory canals**, see 'Veins'. **Mucilage cells**, see 'Epidermis' and 'Mesophyll'.

AXIS

YOUNG STEM

Cork originating in the sub-epidermis except in *Santiria* where it is deeper. Layers of cork, peeling off like paper, in certain species of *Boswellia* and *Commiphora*. Primary **cortex** containing sclerenchymatous idioblasts (presumably identical with the stone cells mentioned by Solereder) in *Bursera* (scattered or in small groups), *Canariellum* (abundant), *Canarium* (sometimes in groups of 6–10; absent from *C. balansae* Engl.), *Crepidospermum*, *Dacryodes*, *Garuga*, *Protium* (often), *Santiria* (small, sometimes in groups), *Trattinickia*, *Triomma*. Cortex traversed longitudinally by secretory canals in *Tetragastris*; including mucilaginous cells in species of *Hedwigia*, *Garuga*, and *Protium*, and sclerenchymatous fibres in *Pachylobus*. **Pericycle** with a composite and continuous ring of sclerenchyma, the latter consisting of arcs of fibres with stone cells between them, in *Aucoumea*, *Bursera* (most species), *Canarium*, *Commiphora* (certain species), *Garuga*, *Santiria*, *Tetragastris*, *Triomma*; with separate arcs of sclerenchyma in *Commiphora* (very small in some species; limited to groups of fibres in the region of the largest secretory canals in *C. fraxinifolia* Bak. and *C. marchandi* Engl.), *Crepidospermum* (almost continuous), *Dacryodes*, *Pachylobus*, *Protium*. Pericyclic sclerenchyma stated by Sabnis (1977) to be absent from *Commiphora mukul* Engl. **Phloem** and **xylem** constituting closed cylinders. Secondary phloem sometimes provided with fibres, notably in *Aucoumea*, *Bursera* (rare), *Canariellum*, *Garuga* (forming a continuous ring), *Santiria macrocarpa* King but not in other species of *Santiria*, and *Trattinickia*. Fibres stated by Guillaumin (839) to be absent from the phloem in *Canarium*. Xylem including small vessels with simple perforations, the vessels sometimes tending to be in radial groups; parenchyma which is chiefly paratracheal, but tangential bands of metatracheal parenchyma have also been recorded in certain species of *Commiphora*; uniseriate or biseriate rays which are often crowded. **Pith** usually homogeneous in *Boswellia*, *Canariellum*, *Canarium*, *Dacryodes*, *Protium*, *Trattinickia*, *Triomma*; heterogeneous in *Aucoumea*, *Garuga*, *Pachylobus*, *Santiria* (outer part sclerified, inner part thin-walled), *Tetragastris*. Pith of *Canarium secundum* A. W. Benn differentiated into a central, non-sclerified region; a completely sclerified region; an outer zone similar to the central one and containing a circle of medullary bundles. Secretory canals recorded in the pith of *Boswellia*, *Canarium balansae* Engl., *Commiphora* (certain species), *Sorindeia juglandifolia* Oliv. var. *dahomensis* A. Chev. (syn. *Pachylobus dahomensis* Engl.) (at the periphery; not occurring in other species of *Pachylobus*). **Medullary bundles** present throughout *Canarium*, but not in the closely related genus *Pachylobus*. The number and arrangement of the medullary bundles varies, even within a single branch in *Canarium*, and is therefore of no specific diagnostic value. **Secretory canals** (see also 'Cortex' and 'Pith') almost invariably present in the phloem, and therefore of diagnostic value for the family, but stated to be absent from the phloem in all organs of '*Scutinanthe boerlagii* Hochr.'.

Certain species of *Commiphora* are characterized by spiny or non-spiny **shoots of limited growth**. Non-spiny short shoots of *C. marchandi* Engl. and *C. orbicularis* Engl. provided with a star-shaped pith and exceedingly large medullary rays.

WOOD (Fig. 79 A-G)

Vessels moderately small (50–100 μ mean diameter) in *Balsamodendron*, *Boswellia*, *Bursera*, *Elaphrium*, *Pachylobus* p.p., *Protium*, and *Tetragastris*, medium-sized (100–200 μ mean diameter) in the other genera, largest in *Garuga*; solitary and in multiples of 2 or 3, occasionally 4 or 5, cells and commonly with some irregular clusters; with a tendency to an oblique radial pattern in some species of *Aucoumea*, *Canarium*, *Commiphora*, *Pachylobus*, *Protium*, *Santiria*, *Tetragastris*, and *Trigonoclamys*; usually varying in number between 4 and 15 per sq. mm., occasionally more numerous, e.g. in *Protium* with 20–40 per sq. mm., fewest (about 5 per sq. mm.) in some species of *Aucoumea*, *Bursera*, *Canarium*, *Garuga*, *Santiria*, and *Trattinickia*. Perforations exclusively simple; intervacular pitting alternate, with hexagonal borders, large, except in some species of *Dacryodes*, *Pachylobium*, *Protium*, *Trigonoclamys*, and *Triomma*, coalescent apertures present in *Aucoumea* and some species of *Canarium*; pits to ray cells and parenchyma large and simple, commonly unilaterally compound. Thin-walled tyloses abundant in some species of *Bursera*, *Canarium*, *Elaphrium*, *Tetragastris*, and *Trattinickia*, and occasionally containing starch grains, crystals, or gum (1154, 2378). Mean member length usually between 0.3 and 0.6 mm.; Webber (2378) notes extremes of 0.1 mm. in *Crepidosperrum* and 0.9 mm. in *Canarium*. **Parenchyma** paratracheal, as sheaths round the vessels, usually rather scanty (Fig. 79 A); when vasicentric, usually limited to a single row, but biseriate in some species of *Canarium* and *Tetragastris*; very sparse in some species of *Bursera*, *Canarium*, *Elaphrium*, *Hemisantiria*, and *Pachylobus*; diffuse parenchyma in addition has been reported (592, 1207, 1208, 2378) in species of *Boswellia*, *Canarium*, *Dacryodes*, and *Protium*; broken bands have been reported (592, 2168, 2378) in some species of *Commiphora*, *Protium*, and *Santiria*. Sometimes containing dark gum; crystals not observed. Sometimes with uniseriate terminal bands in *Dacryodes* and *Protium*, and, according to Spiekerkoetter (2168), in broad tangential bands in *Commiphora subcrenata* A. Peter, *C. mildbraedii* Engl., and *C. heterozygia* A. Peter. Solereder notes that according to J. Möller there are large thin-walled oil cells in the wood of *Bursera aloexylon* Engl. Silica present in *Santiria oblongifolia* Bl. (794). Strands usually of 4 cells, but sometimes of up to 8 cells. Some of the cells reported (2378) to be septate. **Rays** exclusively uniseriate in some species of *Crepidosperrum*, *Dacryodes*, *Hemisantiria*, *Protium*, *Santiria*, *Tetragastris* (938), and *Trigonoclamys*; 2–3 cells wide in most of the other species and up to 4 cells wide in some species of *Boswellia*, *Bursera*, and *Garuga*; Heimsch (938) notes that the rays may be up to 5 or 6 cells wide in a few species; less than 1 mm. high; uniseriate rays few in species with multiseriate rays and composed of both upright and procumbent cells; mostly 4–6 rays per mm. in woods with multiseriate rays, more numerous (up to 12 mm.) in woods with uniseriate rays only; heterogeneous (Kribs's Type II B and III), with 1–3 rows of square or upright marginal cells, up to 4 rows in some species of *Pachylobus*; the marginal cells commonly containing single crystals, such cells sometimes wider tangentially than the non-crystalliferous cells and conspicuous in tangential sections, as in *Balsamodendron*, *Bursera* p.p., *Canarium* p.p., *Commiphora*, *Dacryodes* (2378), *Garuga*, *Protium*, and *Tetragastris*;

procumbent and upright cells commonly containing dark gum. Silica reported (574, 794) in some species of *Canarium*, *Dacryodes*, *Protium*, and *Santiria*. Intercellular spaces moderately distinct in some species. With distinct echelon arrangement and sometimes storied locally in *Canarium* p.p., *Pachylobus* p.p.,

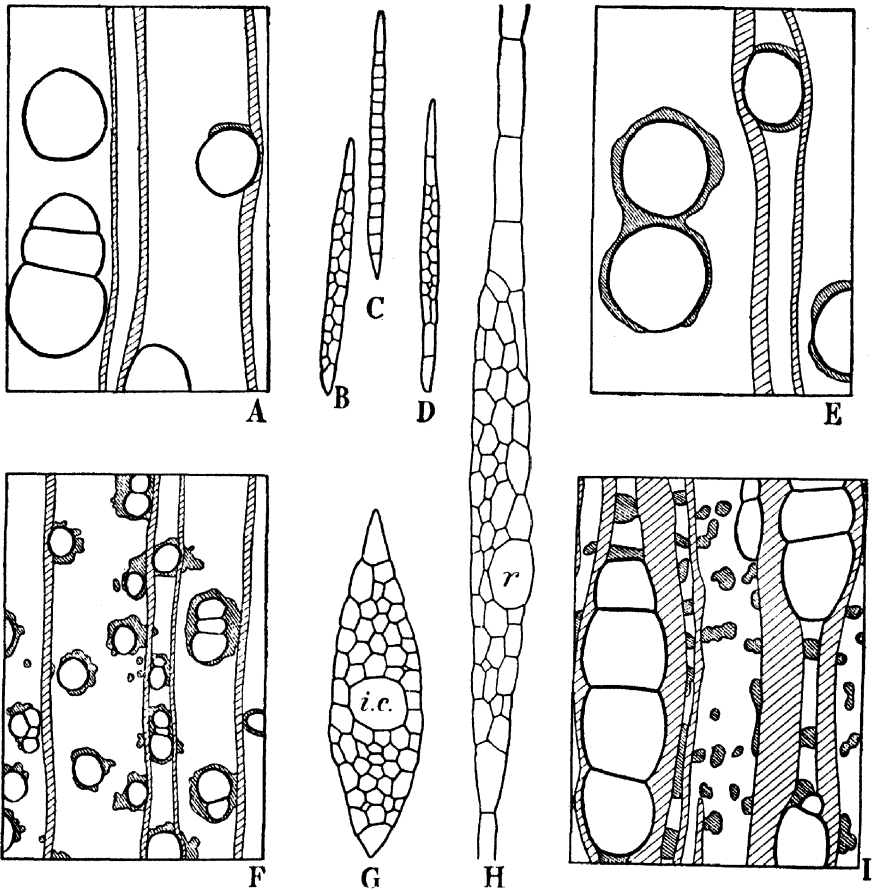


FIG. 79. BURSERACEAE, A-G; TETRAMERISTICACEAE, H-I

A, *Aucoumea klaineana* Pierre. B, *A. klaineana* Pierre. C, *Santiria griffithii* Engl. D, *Pachylobus rostrata* (Bl.) H.J.L. E, *Canarium schweinfurthii* Engl. F, *Protium heptaphyllum* March. G, *Boswellia serrata* Roxb. H, *Tetramerista glabra* Miq. I, *T. glabra* Miq.

i.c. Intercellular canal. r. Cell containing raphides.

most species of *Santiria*, *Trattinickia*, and *Trigonochlamys*. **Fibres** often thin-walled, but with moderately thick walls in *Boswellia*, *Bursera* p.p., *Canarium* p.p., *Dacryodes*, *Pachylobus*, *Protium*, *Santiria* p.p., *Tetragastris*, and *Triomma*; sometimes with a mucilaginous layer and sometimes containing gum; septate in all the material examined, but Spiekerkoetter (2168) states that septa are absent from *Commiphora holziana* Engl. and Heimsch (938) notes their absence from two species of *Canarium*, whose identity is suspect (see under Taxonomic Notes); pits simple, small, slit-like to almost round, and more

numerous on the radial than on the tangential walls; fibres often in regular radial rows; Janssonius (1154) refers to occasional large crystals in the fibres of *Garuga pinnata* Roxb., but these do not appear to be present in all material of this species. Webber (2378) notes the occasional occurrence of starch grains, crystals, and brown, gummy masses. Silica present in *Santiria* spp. (794). Mean length 0.8–1.4 mm. **Intercellular canals** in the secondary rays a constant feature of some species, but of sporadic occurrence in others (Fig. 79 c); small or large; Webber (2378) notes unusually large canals in *Protium puncticulatum* Macbr.; canals observed or reported in at least some species of *Boswellia*, *Bursera*, *Canarium*, *Canariellum* (2378), *Commiphora*, *Dacryodes* (185), *Elaphrium*, *Garuga*, *Protium*, *Tetragastris* (2378), and *Triomma*. Desch (574) notes the absence of radial canals from *Scutinanthe brunnea* Thw., but there appears to be some doubt about the correct identity of this wood. The epithelial cells usually distinctly smaller than the other cells; according to Heimsch (938) the canals in *Commiphora zimmermannii* Engl. are lined with sclerotic cells. Webber (2378) notes abundant tylosoids in *Bursera microphylla* Gray. Traumatic vertical canals have been reported (2378) in *Canarium*, *Protium*, and *Santiria*. Webber (2378) notes the occurrence of gum-filled pith flecks in various species of *Bursera*, *Canarium*, *Crepidosperrum*, *Dacryodes*, *Protium*, and *Tetragastris*, 'suggesting that traumatic vertical canals may be present under certain conditions'. Besson (186) shows rather low ash and silica percentages for woods of this family.

ROOT

Examined only in *Aucoumea* and *Canarium* spp. **Cortex** containing a continuous or interrupted zone of sclerenchyma. Numerous layers of discontinuous sclerenchyma occur in *Aucoumea*. **Phloem** containing frequent secretory canals of large diameter, and a few fibres. **Xylem** provided with vessels of large diameter filled with tyloses.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Burseraceae constitute an anatomically homogeneous group. Guillaumin (839) considers that they have affinities with the Rutaceae, Anacardiaceae, Simarubaceae, Cneoraceae, Meliaceae, Coriariaceae, Sapindaceae, and Hippocastanaceae, but of these, the most marked affinities are with the Rutaceae, Anacardiaceae, Meliaceae, and Simarubaceae. Guillaumin (838) has also drawn attention to the fact that the anatomical characters of *Pachylobus dahomensis* Engl. differ somewhat from those of other species of *Pachylobus*. For this reason he suggests that this species may have been wrongly included in the Burseraceae, and that it shows closer affinities with the Anacardiaceae and in particular with *Sorindeia*. In another paper Guillaumin (840) has shown that, on anatomical grounds, *Canarium sumatranum* Boerlage et Koorders is correctly included in *Canarium*. While anatomical characters such as the occurrence of resin canals in the phloem of both families have been used as evidence of the close relationship of the Burseraceae and Anacardiaceae, Engler (643) considers that the constant floral differences between the two groups are too great to justify the view that there is any very

close affinity between them. Hutchinson treats the families in separate orders, which are, nevertheless, regarded as being phylogenetically related.

(ii) FROM WOOD STRUCTURE

Both Webber (2378) and Heimsch (938) consider that the Rutaceae, Simarubaceae, Meliaceae, Sapindaceae, Burseraceae, and Anacardiaceae form a natural group. Heimsch states that 'The Burseraceae and Anacardiaceae are highly similar in xylem structure and together are distinct from the others', basing this opinion mainly on the occurrence of radial intercellular canals, less advanced ray types, the lack of banded parenchyma other than terminal, the type of ray-vessel pitting, and the common occurrence of septate fibres in both families. Webber, on the other hand, concludes that 'the wood structure of the Burseraceae rather than presenting evidence for grouping this family with the Anacardiaceae instead of with the Simarubaceae, Rutaceae and Meliaceae, is more suggestive of the probable common ancestry of all five families'. She considers the Burseraceae and Anacardiaceae to be the least specialized of this group and suggests that the traumatic canals of the Simarubaceae and Rutaceae may indicate their origin from plants such as the Burseraceae and Anacardiaceae that have normal intercellular canals in their rays.

Janssonius (1154, vol. v, p. 464) notes a close similarity between the woods of this family and those of a group of the Euphorbiaceae (see 'Phyllanthoideae', Group B, p. 1221) that includes the genera *Acalypha*, *Antidesma*, *Bischofia*, *Bridelia*, and *Glochidion*. No radial canals, such as are characteristic of the Burseraceae, however, occur in this group.

Webber (2378) has considered the evidence of wood anatomy on the internal specialization of the family. She has found that there is no evidence from the wood (a) that the Asiatic species of *Protium* are more specialized than the American species of this family, (b) that species having many leaflets are more specialized than those with few, or (c) that the woods of *Canarium* and *Commiphora* are more specialized than those of *Protium*. From the basic similarity between the woods of all the genera she concludes that, in this family, specialization in the structure of the fruits, flowers, and leaves has proceeded at a more rapid rate than in the woods.

The wood of *Canarium sumatranum* does not differ significantly from that of other species of *Canarium*. Heimsch (938) notes that the woods of *C. bengalense* Roxb. and *C. commune* Linn. differ not only from other species of *Canarium* but from the family as a whole in such features as the type of parenchyma and the absence of septate fibres and suggests that they may be wrongly placed in this family.

ECONOMIC USES

Frankincense is a gum resin obtained from the bark of *Boswellia carteri* Birdw. Myrrh is a similar substance from various species of *Commiphora*. A gum resin, also used as incense, is obtained from *Protium heptaphyllum* (Aubl.) March. The wood of various species of *Bursera* is perfumed. Black Dammar is the product of *Canarium strictum* Roxb.

The family includes one very important timber tree, *Aucoumea klaineana*

Pierre, which furnishes the Gaboon Mahogany or Okoumé of commerce. The timber is very extensively used for veneers and plywood.

The timbers of the other genera are also light and easy to work and some of them are used locally for packing-cases, cheap furniture and planking.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aucoumea, Boswellia, Bursera, Canariellum, Canarium, Commiphora, Crepidospermum, Dacryodes, Garuga, Hedwigia, Pachylobus, Protium, Santiria, Scutinanthe, Tetragastris, Trattinickia, Triomma.

(ii) FOR WOOD STRUCTURE

Aucoumea, Balsamodendron, Boswellia, Bursera, (Canariellum), Canarium, Commiphora, (Crepidospermum), Dacryodes, Elaphrium, Garuga, Hemisantiria, Pachylobus, Protium, Santiria, (Scutinanthe), Tetragastris, Trattinickia, Trigonochlamys, and Triomma.

LITERATURE

(i) *On General Anatomy*

Engler 643, Guillaumin 838, 839, 840, Sabnis 1977, Solereder 2163, Spiekerkoetter 2168.

(ii) *On Wood Structure*

Beekman 167, den Berger 179, 182, Besson 186, Br. Hond. F.D. 274, Chevalier *et al.* 312, Collardet 448, Cooper 461, Dadswell 525, Desch 574, Dixon 592, Gonggrijp 794, Heimsch 938, Howard 1088, Janssonius 1154, Jentsch 1172, Kanehira 1207, 1208, Kribs 1283, Lecomte 1332, Martin-Lavigne 1450, Méniard 1491, Pearson and Brown 1679, Pfeiffer J. Ph. 1713, Record 1780, 1783, 1787, 1801, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Riera 1937, Spiekerkoetter 2168, Stone 2202, 2207, Torres 2269, Webber 2377, 2378, Williams 2430.

87. MELIACEAE

(FIG. 77 on p. 334; FIG. 80 on p. 350; FIG. 81 on p. 354)

SUMMARY

(i) GENERAL

A family from tropical and warm temperate regions consisting almost exclusively of trees or shrubs. The **hairs** are of various kinds. (i) Unicellular or uniseriate. (ii) Two-armed. (iii) Stellate. (iv) Peltate. (v) Glandular hairs of various types. The **leaf** is always dorsiventral, and the lamina is particularly characterized by the presence of variously shaped **secretory cells** containing resin, which are usually situated at the boundary between the palisade and spongy mesophyll. Secretory cells are sometimes present in the cortex and pith of the axis as well, while **secretory cavities** occur in the same positions in a few genera. **Stomata** in the leaf have been recorded only on the lower surface; they are ranunculaceous. **Hypoderm**, which is confined to the upper side of the leaf, has been observed only in *Carapa* sp. and in *Entandrophragma*. The **mesophyll** of a few genera includes 'spicular cells' and crystal idioblasts. The **midrib** contains variously orientated, isolated, collateral bundles in *Khaya*, *Melia*, *Trichilia*, and *Turraea*, but a closed ring

of xylem is present in *Entandrophragma*. The **petiole** of species with simple leaves, in transverse sections, exhibits an arc of bundles or a single arc-shaped vascular strand: in pinnate leaves there is a closed vascular ring. Medullary bundles have been recorded in the petiole in a few genera. In the axis the **cork** originates in the sub-epidermis; the **cortex** contains stone cells of various types (sometimes present in the pith as well); the **pericycle** is characterized by separate crescentic strands of fibres, which are, however, very close together in some species. The **xylem** and **phloem** in young stems

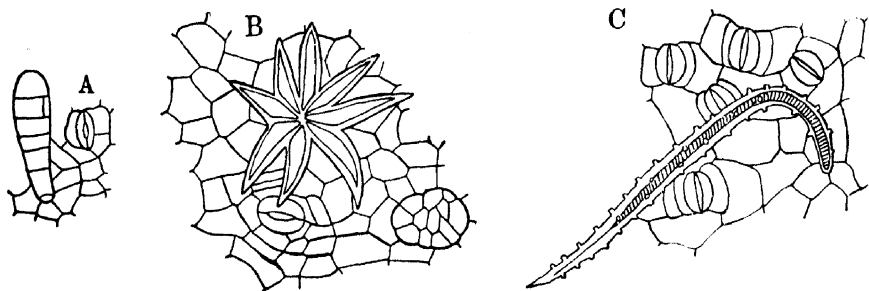


FIG. 80. MELIACEAE, A; RUTACEAE, B; DICHAPETALACEAE, C

A, Lower epidermis of the leaf of *Cedrela toona* Roxb. with a glandular hair. B, Lower epidermis of the leaf of *Flindersia maculosa* (Lindl.) Benth. with a peltate and a glandular hair. C, Lower epidermis of the leaf of *Tapura amazonica* Poepp. et Endl.—By Solereder.

constitute a closed cylinder traversed by narrow rays. The secondary phloem contains fibres, either scattered, in small groups, or in bands. **Crystals**, both solitary and clustered, are common in the tissues of all of the organs.

(ii) WOOD

Vessels moderately small to medium-sized; radial multiples of 2 or 3 cells common; perforations exclusively simple; intervacular pitting typically minute, but occasionally larger; pits to ray cells similar; members of medium length. **Parenchyma** most characteristically paratracheal (vasicentric, aliform, or confluent) and often with terminal in addition; diffuse parenchyma sometimes present and often consisting of crystalliferous cells; broad, moderately regular and apparently apotracheal bands characteristic of some species; sometimes storied. **Rays** usually exclusively uniseriate or 2–4 cells wide, but considerably wider (up to 9 cells) in some species; uniseriate rays usually rare in woods with multiseriate rays; mostly heterogeneous, with 1–2 marginal rows, but homogeneous in some genera; often distinctly storied or in echelon. **Fibres** with simple or narrowly bordered pits, septate in a majority of species; of medium length to moderately short. **Intercellular canals** of the traumatic vertical type occur sporadically.

LEAF

Dorsiventral. **Hairs** include the following kinds. (i) Simple, unicellular in *Aitonia*, *Chisocheton*, *Dysoxylum*, *Ptaeroxylon*, *Trichilia*, *Turraea*. (ii) Uniseriate in *Cedrela* and *Melia*. (iii) Two-armed hairs in certain species of *Amoora*, *Dysoxylum*, *Epicharis*, and occasionally in other genera as well.

(iv) Stellate hairs in *Aglaia*, *Melia*, *Pterorhachis*, *Trichilia*. (v) Peltate scales, sunk in small pits in the strongly cuticularized leaf surface, in *Aglaia*, *Amoora*. (vi) Glandular hairs, always multicellular but variously shaped, in *Cabrarea*, *Carapa*, *Cedrela* (Fig. 80 A), *Entandrophragma*, *Melia*, *Ptaeroxylon*, *Turraea*. Cells of the **epidermis** mucilaginous in *Chukrasia* sp. and in the Cedreleae; papillose in certain species of *Ekebergia*, *Heynea*, *Walsura*. **Stomata** confined to the lower surface; ranunculaceous in certain species of *Aitonia*, *Carapa*, *Cedrela*, *Khaya*, *Melia*, *Ptaeroxylon*, *Swietenia*, *Trichilia*, *Turraea*. **Hypoderm** below the upper epidermis recorded only in species of *Aglaia*, *Carapa*, *Entandrophragma*, *Sandoricum*. **Mesophyll**. Palisade tissue 1-layered in species of *Melia* and *Turraea*; more than 1-layered in *Carapa moluccensis* Lam., *Entandrophragma* sp., *Khaya* sp., *Trichilia* (up to 4-layered). Sclerenchymatous idioblasts present in the mesophyll in certain species of *Dysoxylum* and in *Khaya senegalensis* A. Juss. Vascular bundles of the **midrib** exhibiting a considerable range of structure in different genera and species; with 2 bundles in most species of *Turraea*, but united to form a single strand in 1 species; with 2 superimposed bundles in *Khaya senegalensis* and *Melia volkensii* Gürke, with an arc-shaped strand with incurved ends in *Trichilia*; with a triangular strand with incurved ends towards the adaxial side in *Entandrophragma casimirianum* De Willd. et Dur. (syn. *E. candolleianum* Willd. et Dur.). **Petiole** with 3 bundles entering the base, the bundles becoming united towards the distal end to form a single crescent-shaped strand with incurved ends in most species of *Turraea* (Fig. 77 D). Medullary bundles occur in certain species of *Cedrela*, *Soyimida*, *Trichilia*, *Vavaea*, and *Walsura*; and have been described by Spiekerkoetter (2168) in *Turraea*. According to Solereder the petioles of species with simple leaves, especially in *Quivisia*, *Turraea*, and *Walsura*, exhibit, in transverse sections, an arc of bundles, and those with pinnate leaves a ring of bundles. This may in general be true but the matter needs further investigation. A cylindrical vascular strand was noted in *Khaya senegalensis* A. Juss. (Fig. 77 A). **Secretory cells** of various sizes and shapes occur throughout the family. They are sometimes branched, and most commonly to be found at the boundary between the palisade and spongy mesophyll, although confined to the region of the bundles in *Megaphyllaea*, and recorded in the centre of the midrib and in the petiole of *Entandrophragma casimirianum*. **Crystals**, both solitary and clustered, common; their size, nature, and distribution believed to be of value for specific diagnosis. Skutch (2127) has recently investigated a compound leaf of *Guarea* which exhibits annual increments of growth.

AXIS

YOUNG STEM

Stem surface papillose in *Melia volkensii* Gürke. **Cork** invariably arising in the sub-epidermis in all of the species examined; thickening of the cork cells very variable in different genera and species, e.g. considerably thickened in *Trichilia* and *Turraea*, weakly suberized in *Khaya senegalensis* A. Juss. Intumescences which arise from the phelloderm and consist of thin-walled phelloid cells filled with fatty material occur on the stem surface in *Khaya ivorensis* A. Chev. and *K. senegalensis* A. Juss. They have been described by Ossowski (1643). **Cortex** containing stone cells. The latter solitary in certain species of

Amoora, *Entandrophragma*, *Hearnia*, *Khaya*, and *Vavaea*; sometimes grouped in *Cabralea*, *Chisocheton*, *Dasycoleum*, *Megaphyllaea*, and *Synoum*; branched in *Aglaia* sp.; arranged in a ring in certain species of *Amoora* and *Sandoricum*. Slightly sclerosed parenchyma sometimes present in *Guarea* and *Trichilia*. Resinous secretory cells occur in the cortex of *Entandrophragma casimirianum* De Willd. et Dur. (syn. *E. candolleianum* Willd. et Dur.), *Khaya senegalensis* A. Juss., and probably other species. **Pericycle** nearly always containing isolated strands of fibres, but a composite and continuous ring recorded in *Cabralea* sp. **Phloem** and **xylem** constitute closed cylinders traversed by narrow rays. Secondary phloem containing fibres, either scattered, in small groups, or in bands or rings, e.g. in isolated groups in some species of *Turraea*, but forming tangential bands in other members of this genus; with concentric rings of fibres in *Khaya senegalensis* A. Juss. and *Melia volkensii* Gürke. Vessels with simple perforations. **Pith** very variable in size; homogeneous or heterogeneous, variations in this respect being exhibited by different members of a single genus. Perimedullary region clearly differentiated from the remainder of the pith in some species, but not in others. Spiekerkoetter (2168) suggests that this character may be of specific diagnostic value. Resinous secretory cells present in the pith of *Entandrophragma casimirianum* and secretory cells in *Melia azedarach* Linn. Groups of stone cells or prosenchymatous elements recorded in the pith of certain species of *Cabralea*, *Chisocheton*, *Hearnia*, *Megaphyllaea*, and *Sandoricum*. **Secretory cells**, see 'Cortex' and 'Pith'.

FRUIT STALK

Fruit stalks stated by Solereder to be polystelic in *Swietenia mahogani* Linn.

BARK

According to Wenzel (2412) the tanniniferous bark of *Carapa moluccensis* Lam. exhibits the following characters. Bark covered externally by a layer of **cork** 275–400 μ broad; cork composed of radially arranged cells of variable size and form and commonly containing cluster crystals. **Rays** extending to the inner boundary of the cork layer, mostly 2 cells wide but sometimes up to 4 and very rarely 5 cells wide; up to 2, but mostly 1 mm. tall. Ray cells twice as long in radial as in tangential diameter. Cells of the **phloem parenchyma** with thicker walls than those of the rays; vertically elongated, containing rhomboidal crystals of calcium oxalate. Phloem parenchyma traversed by tangential bands of sclerenchyma; bounded externally by a tissue of disorganized sieve tubes (Keratenchym). Calcium oxalate **crystals** sometimes of unusual form, and capable of being mistaken for stone cells. For the histology of *Cocillana* and substitute (*Guarea*) barks see 'Economic Uses'.

WOOD (Fig. 81)

Vessels usually moderately small to medium-sized (50–200 μ , mean tangential diameter), very small (less than 50 μ) in *Ptaeroxylon*, large (more than 200 μ) in at least some specimens of *Amoora*, *Carapa*, *Dysoxylum*, *Entandrophragma*, *Khaya*, and *Lovoa*; multiples of 2 or 3 cells common, with some multiples of 4–6 cells, in *Cabralea*, *Heynea*, *Owenia*, *Ptaeroxylon*, *Trichilia*, *Turraea*, and *Walsura* p.p.; clusters moderately common in *Heynea*, *Melia*, *Synoum*, *Turraea*, and *Walsura* p.p.; with a tendency to oblique arrangement

locally in *Heynea*, *Turraea*, and *Vavaea* and in distinct radial rows in *Cipadessa* (938), *Ptaeroxylon*, and *Pterorhachis* (938); varying in number from fewer than 5 per sq. mm. in the species with the larger vessels to about 20 per mm.; more numerous in *Ptaeroxylon*; ring-porous or semi-ring-porous in some species of *Cedrela* and *Melia*; spiral thickening present in *Melia* and sometimes in the smaller vessels of *Cedrela*. Perforations exclusively simple. Intervascular pitting alternate; minute except in *Amoora*, *Aphanomixis*, *Cedrela*, *Ekebergia*, *Melia*, *Pseudocarapa*, and *Ptaeroxylon*, and sometimes with coalescent apertures in these genera; pits to ray cells similar to the intervacular pitting, Heimsch (938) states that this pitting 'tends to be oblong or gash-like' in *Cedrela* and *Melia*, but this could not be confirmed in the material examined. Tyloses absent, deposits of gum common. Mean member length 0.3–0.7 mm. **Parenchyma** very variable in type and amount, terminal, diffuse, vasicentric, aliform, confluent, and broad bands being all represented in different genera, and even the species of single genera are often distinguished by widely different forms. Paratracheal parenchyma is always present, except in *Ptaeroxylon*, and is typically predominant; even in species with regular and apparently metatracheal bands the parenchyma in many cases becomes aliform or confluent where it is locally less abundant. Terminal bands, often conspicuous and 4 or more cells wide, present in *Azadirachta*, *Carapa*, *Cedrela*, *Chukrasia*, *Dysoxylum*, *Ekebergia*, *Entandrophragma*, *Epicharis*, *Heynea*, *Khaya* (sporadic), *Lansium* (938), *Owenia*, *Pseudocedrela*, *Ptaeroxylon*, *Soymida*, *Swietenia*, *Trichilia*, *Turraea*, *Walsura* (938), and *Xylocarpus*; Kribs (1285) reports terminal parenchyma also in *Cipadessa* and *Sandoricum*; diffuse parenchyma, sometimes containing crystals, and in some genera consisting almost entirely of scattered files of crystalliferous cells, present in *Azadirachta*, *Carapa* p.p., *Cedrela* (Fig. 81 N), *Chukrasia*, *Guarea* (rare), *Khaya* p.p., *Lovoa*, *Melia* p.p., *Owenia*, *Pseudocarapa*, *Pseudocedrela*, *Ptaeroxylon*, *Sandoricum*, *Soymida*, *Swietenia* p.p., *Synoum*, and *Xylocarpus*, and reported by Heimsch (938) in *Vavaea* and *Walsura*; parenchyma, other than terminal and diffuse as described above (a) absent from *Ptaeroxylon*, (b) scanty to vasicentric in *Chukrasia*, *Cipadessa*, *Ekebergia*, *Epicharis*, *Khaya*, *Melia*, *Owenia*, *Pseudocedrela*, *Swietenia* (Fig. 81 J), *Turraea*, *Turraeanthus*, and *Xylocarpus*; vasicentric to predominantly aliform in *Azadirachta*, *Carapa*, *Cedrela*, *Lovoa* (Fig. 81 I), *Pseudocarapa*, and *Vavaea*, (c) predominantly aliform or confluent, or in moderately regular bands in *Aglaia*, *Guarea* (Fig. 81 E), '*Moschoxylum*', and *Trichilia*, and (d) consistently in bands in *Cabralea*, *Lansium*, *Reinwardtiodendron*, *Synoum*, and *Walsura* (Fig. 81 A); single cells scattered among the fibres (diffuse) in some species of *Cedrela*, *Pseudocarapa*, and *Pseudocedrela*. Crystals present in chambered cells in *Azadirachta*, *Cabralea*, *Chisocheton*, *Chukrasia*, *Cipadessa*, *Dysoxylum*, *Ekebergia*, *Entandrophragma*, *Epicharis*, *Guarea*, *Melia*, '*Moschoxylum*', *Owenia*, *Ptaeroxylon*, *Reinwardtiodendron*, *Sandoricum*, *Trichilia*, *Turraeanthus*, *Vavaea*, and *Xylocarpus*, and in the ordinary cells in some other species; silica present in *Aphanomixis grandifolia* Bl. and *Chisocheton* spp. (794). Sometimes containing gum. According to Welch (2396) the parenchyma of *Dysoxylum fraserianum* Benth. contains a volatile oleo-resin that may cause 'sweating' and spoil a polished surface, particularly in timber not properly seasoned. Usually storied in woods with storied rays and sometimes where the rays are not storied, e.g. in *Carapa*. Strands

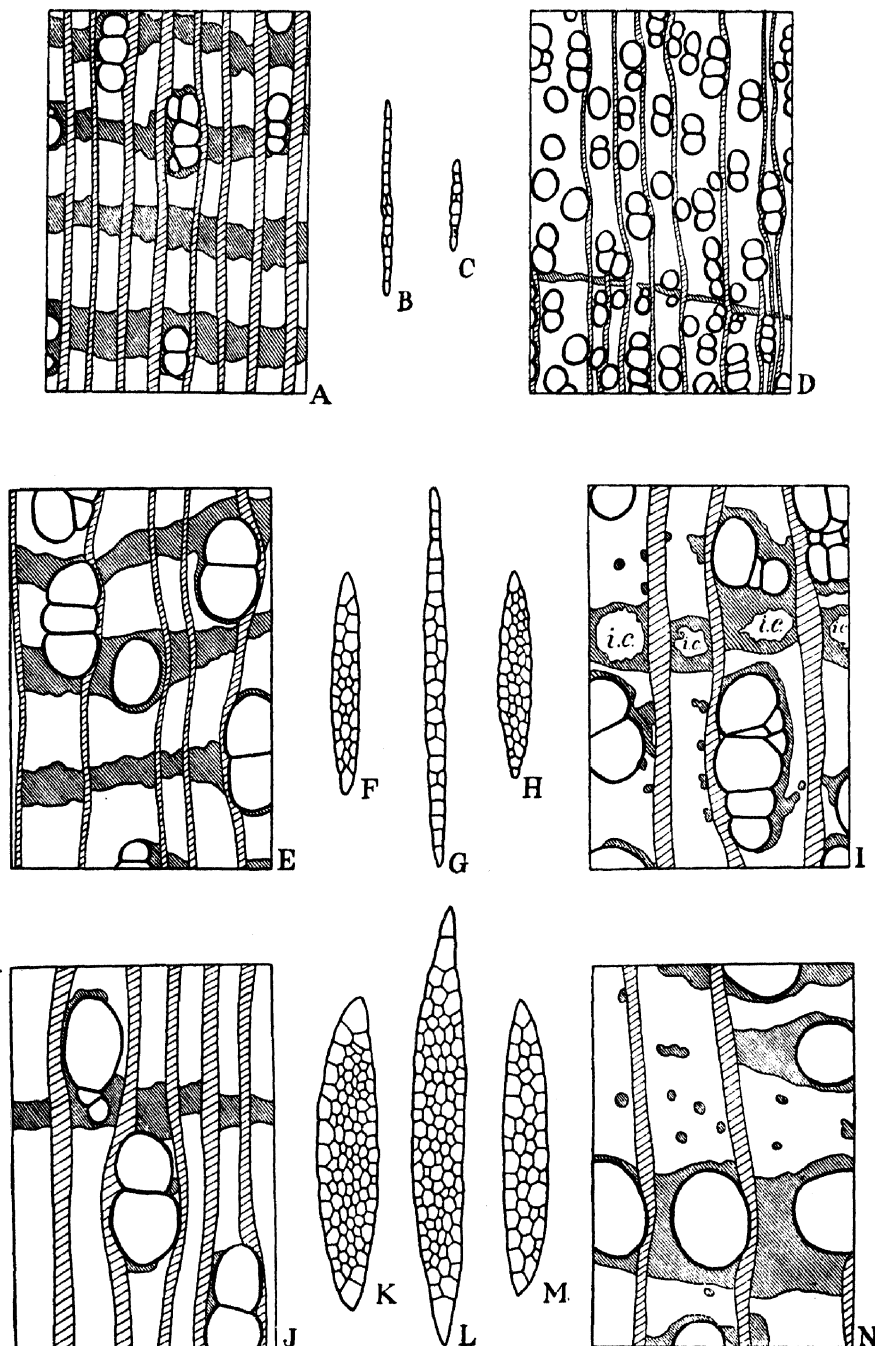


FIG. 81. MELIACEAE

A, *Walsura villosa* Wall. B, *Amoora maingayi* Hiern. C, *Ptaeroxylon obliquum* Radlk. D, *P. obliquum* Radlk. E, *Guarea cedrata* (A. Chev.) Pellegr. F, *Chukrasia tabularis* Juss. G, *Guarea cedrata* (A. Chev.) Pellegr. H, *Lovoa klaineana* Pierre. I, *L. klaineana* Pierre. J, *Swietenia macrophylla* King. K, *S. macrophylla* King. L, *Khaya ivorensis* A. Chev. M, *Cedrela odorata* Linn. N, *C. odorata* Linn. i.c. Intercellular canal.

typically of 8 cells, but commonly with strands of 4–6 cells in some species of *Ekebergia*, *Entandrophragma*, *Heynea*, *Melia*, *Trichilia*, and *Turraeanthus*; strands of up to 12 cells common in some specimens of *Dysoxylum*. **Rays** exclusively uniseriate or nearly so in *Aglaia* p.p., *Amoora* p.p., *Aphanomixis*, *Cabralea* p.p., *Cipadessa*, *Dysoxylum* p.p., *Elutheria* (1886), *Guarea* p.p., *Lansium*, *Pseudocarapa*, *Ptaeroxylon*, *Pterorhachis* (938), *Synoum*, *Trichilia* p.p., and *Turraea* p.p. (938); the remainder mostly 2–3 cells wide, but up to 4–6 cells wide in some species of *Carapa*, *Entandrophragma*, *Khaya*, *Lovoa*, *Owenia*, *Turraeanthus*, *Walsura*, and *Xylocarpus* and up to 7–9 cells wide in some species of *Khaya* and in *Melia*; commonly more than 1 mm. in height in some species of *Amoora*, *Carapa*, *Dysoxylum*, and *Khaya*; uniseriate rays usually rare in species with multiseriate rays and commonly only 1 or 2 cells high; varying from all square or upright cells to all procumbent cells; uniseriates more numerous in *Khaya* than in *Entandrophragma* or *Swietenia*; Panshin (1650) describes the rays of *Khaya* and *Soymida* as being of 2 sizes; mostly between 4 and 14 per mm., up to 20 per mm. in *Cipadessa* and *Turraea*; rays, where exclusively uniseriate, varying from heterogeneous (Kribs's Type III) to homogeneous (Kribs's Type III), often even within 1 genus; typically homogeneous in species of *Aphanomixis*, *Guarea*, *Pterorhachis*, and *Trichilia* (938). Multiseriate rays commonly heterogeneous (Kribs's Type II B), with 1 or 2 marginal rows of square or upright cells, but with 4 or more rows in *Sandoricum* and *Vavaea*; species with rays 2–3 cells wide commonly with several uniseriate marginal rows, but with only the extreme 1 or 2 rows composed of square or upright cells; homogeneous (Kribs's Types I and II) in *Ekebergia* p.p., *Entandrophragma* p.p., *Guarea*, *Lovoa* p.p., *Melia*, *Ptaeroxylon*, *Reinwardtiadendron*, *Turraeanthus*, and *Walsura*, and nearly homogeneous in some species of *Aglaia*, *Azadirachta*, *Cedrela*, *Chisocheton*, *Dysoxylum*, '*Moschoxylum*', *Soymida*, *Toona*, and *Trichilia* and, according to Heimsch (938), in occasional specimens of *Swietenia* and *Turraea*; crystals common in the marginal cells of *Carapa*, *Cedrela*, *Entandrophragma*, *Khaya*, *Owenia*, *Pseudocedrela*, *Soymida* (1285), *Swietenia*, and *Xylocarpus*; Janssonius (1154) refers to occasional druses in *Cedrela*; cells often containing gum; silica present in *Aphanomixis grandifolia* Bl. and *Chisocheton* spp. (794). Storied in most specimens of *Pseudocedrela*, *Ptaeroxylon*, *Swietenia*, and *Xylocarpus* and in some species of *Carapa*, e.g. *C. moluccensis* Lam., and *Entandrophragma*, e.g. *E. cylindricum* Sprague, and occasionally, according to Record (1851), in *Cedrela*, *Chukrasia*, and *Khaya*; in echelon in some other genera. **Fibres** with pits usually confined almost entirely to the radial walls, simple or with very narrow borders.¹ Septate in most of the genera but non-septate in *Cedrela*, *Chukrasia*, *Ekebergia*, *Heynea*, *Lovoa*, *Melia*, *Odontandra* (938), *Owenia*, *Pterorhachis* (938), *Quivisia* (1285), *Sandoricum*, *Soymida*, *Trichilia*, *Turraea*, *Turraeanthus*, and *Walsura*; some-

¹ There appears to be some difference of opinion as to the nature of the pitting in the fibres in this family. Kribs (1285) uses the presence of simple pits as one of the characters by which he distinguishes the genera of his proposed sub-families Swietenioideae and Lovoinoideae, i.e. *Carapa*, *Cedrela*, *Chukrasia*, *Entandrophragma*, *Khaya*, *Lovoa*, *Pseudocedrela*, and *Soymida*. Janssonius (1154) describes the pits as simple in *Carapa* and *Walsura* and bordered in *Aglaia*, *Amoora*, *Cedrela*, *Chisocheton*, *Dysoxylum*, and *Melia*. Panshin (1650) describes the pits of *Chukrasia* as bordered and those of *Khaya* and *Entandrophragma* as bordered in some species. Many other discrepancies in the literature might be cited.

times with a few septate fibres in *Cedrela* and *Chukrasia* (1285). Sometimes containing gum. Walls usually thin to moderately thick, but thick in *Aglaia*, *Lansium*, *Owenia*, *Pseudocarapa*, and *Soymida*. Mean length 0.6–1.9 mm. **Intercellular canals** of the vertical, traumatic type have been reported in *Carapa*, *Cedrela*, *Dysoxylum*, *Entandrophragma*, *Khaya*, *Lovoa*, *Melia*, *Sandoricum*, and *Swietenia*. Groom (826) states that in *Khaya*, *Lovoa*, and *Swietenia* small canals are usually lysigenous, but those in well-developed bands are schizo-lysigenous or schizogenous and that the contents give reactions typical of wound gum. **Growth ring** development has been studied by Coster (481) in *Azadirachta*, *Melia*, *Swietenia*, and *Toona*, by Chowdhury (415) in *Cedrela*, and by Hummel (1109) in *Entandrophragma* and *Khaya*. Besson (186) shows a relatively high percentage of silica for *Entandrophragma candollei* Harms.

ROOT

The erect, peg-like **pneumatophores** of *Amoora cuculata* Roxb. and *Carapa moluccensis* Lam. have been investigated by Groom (826) and Liebau (1368). They arise from horizontal roots as horn-like wings produced by the activity of the cambium, and continue to grow in height and thickness by means of a cambium. Forked pneumatophores sometimes arise by the fusion of two situated side by side. **Lenticels** are always present. The **xylem** of the pneumatophores consists of vessels, fibres, and parenchyma arranged in periclinal arches, but the structure becomes more complex with increase in age. The scanty vessels are partly blocked by callus-like plugs in *Amoora*. Groundwork of the wood composed of thin-walled fibres and parenchyma, or of parenchyma alone.

Gallager (736) has recorded a few facts about the roots of twenty-two species of Meliaceae, without including any features of great taxonomic interest beyond the occurrence of secretory cells in all of the species examined except in *Cedrela*, but even here their absence was not definitely affirmed.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The family is anatomically similar to and undoubtedly has affinities with the Rutaceae and Burseraceae. The boundaries between these families are, in fact, by no means well defined, and taxonomists have not always agreed in which of them some of the genera should be placed. *Chloroxylon*, for example, has been variously included in the Rutaceae and Meliaceae. The anatomical features are not conclusively more in favour of one of these views than the other. *Aitonia* and *Ptaeroxylon* also have a somewhat indefinite status since they have been placed in the Sapindaceae by some authors and in the Meliaceae by others. *Flindersia* is yet another genus of uncertain position, which in this book has been described under Rutaceae.

(ii) FROM WOOD STRUCTURE

Kribs (1285) suggests that *Carapa*, *Cedrela*, and *Xylocarpus* should be placed in the sub-family Swietenioideae and that *Lovoa* should be set aside by itself in a sub-family Lovoinoideae. Panshin (1650) also comments on the different structure of *Lovoa*. Kribs considers that the Swietenioideae (as thus

re-defined by himself) is the only sub-family in which the genera form a distinct homogeneous group in respect to anatomical and morphological characters and suggests that it should be raised to the rank of a family.

Kribs notes that of the four genera with simple leaves, *Reinwardtiidendron*, *Turraea*, *Vavaea*, and *Quivisia*, the wood anatomy of the three latter is closely similar and is relatively more primitive than that of the other genera, but that the wood of *Reinwardtiidendron* closely resembles that of *Lansium*.

Commenting on the confusion existing over the identity of certain genera of the Melioideae, he lists characters of the wood by which *Aphanomixis* can be separated from *Amoora*, *Azadirachta integrifolia* Merr. from *Melia*, and *Carapa* from *Xylocarpus*.

Kribs considers that, on the basis of the anatomy of their woods, the genera *Chloroxylon*, *Flindersia*, and *Ptaeroxylon* should be placed in the Rutaceae.

Panshin finds that the wood anatomy of *Entandrophragma* spp. bears out the separation of the four sub-genera established by Harms.

The woods of *Cedrela* and *Toona* are indistinguishable. Janssonius (1154) draws attention to the marked difference between the woods of *Cedrela* and *Melia* and those of the other genera and suggests that these two genera should be placed in a separate family. Heimsch (938) considers that the Meliaceae, Rutaceae, Simarubaceae, Sapindaceae, Burseraceae, and Anacardiaceae constitute a more or less natural group of plants.

ECONOMIC USES

This family is possibly of greater importance as a source of hardwood timber than any other. It includes several woods that are well known all over the world, such as Mahogany (*Swietenia*), African Mahogany (*Khaya*), Sapele Mahogany (*Entandrophragma*), Spanish Cedar (*Cedrela*), and African Walnut (*Lovoa*), and several others that, though less important, are well known to commerce outside the countries where they are grown, e.g. Bosse (*Trichilia*), Rose Mahogany (*Dysoxylum*), various Cedars (*Cedrela* and *Toona*), and Crabwood or Andiroba (*Carapa*). Many others are of importance locally. The best-known timbers are typically red in colour, lustrous, and easy to work; they are often highly figured and some, e.g. the True and African Mahoganies, are unusually free from distortion under changing conditions of moisture. Such characters make these woods eminently suitable for cabinet work. Some of the woods make excellent constructional timber, e.g. the Entandrophragmas, and are often used locally for such purposes. The bark of *Carapa moluccensis* Lam. yields tannin, and that of *Guarea rusbyi* Rusby, known to pharmacognosists as Cocillana, possesses medicinal properties resembling those of Ipecacuanha. The microscopical characters of Cocillana and related barks have been described by Ballard (115). The tanniniferous bark of *Carapa moluccensis* is described above on p. 352.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aglaia, Aitonia, Amoora, Cabralea, Carapa, Cedrela, Chisocheton, Chloroxylon, Chukrasia, Dasycoleum, Dysoxylum, Ekebergia, Entandrophragma, Epicharis, Guarea, Hearnia, Khaya,* Megaphyllaea, Melia,* Ptaeroxylon,

Pterorhachis, *Quivisia*, *Sandoricum*, *Soymida*, *Swietenia*,* *Synoum*, *Trichilia*,* *Turraea*,* *Vavaea*, *Walsura*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Aglaiia, *Amoora*, *Aphanomixis*, *Azadirachta*, *Cabranea*, *Carapa*, *Cedrela*, *Chisocheton*, *Chukrasia*, (*Cipadessa*), *Dysoxylum*, *Ekebergia*, (*Elutheria*), *Entandrophragma*, *Epicharis*, *Guarea*, *Heynea*, *Khaya*, *Lansium*, *Lovoa*, *Melia*, '*Moschoxylum*', *Owenia*, *Pseudocarapa*, *Pseudocedrela*, *Ptaeroxylon*, (*Pterorhachis*), (*Quivisia*), *Reinwardtiadendron*, *Sandoricum*, *Soymida*, *Swietenia*, *Synoum*, *Trichilia*, *Turraea*, *Turraeanthus*, *Vavaea*, *Walsura*, and *Xylocarpus*.

LITERATURE

(i) *On General Anatomy*

Ballard 115, Gallager 736, Groom 826, Harms 904, Kienholz 1236, Ledoux 1336, 1337, 1338, Liebau 1368, Ossowski 1643, Skutch 2127, Spiekerkoetter 2168, Wenzel 2412.

(ii) *On Wood Structure*

Aubréville 49, 50, 51, 53, 54, Baker 104, Becking 164, Beekman 167, Benoist 170, den Berger 179, 182, Besson 186, Boulger 244, B.H. For. D. 274, Burgerstein 310, 312, Busch 322, Chalk *et al.* 360, 364, Chattaway 368, Chowdhury 411, 415, Collardet 449, 450, Cooper and Record 461, Coster 481, Dadswell 525, 530, Dixon 592, Duchesne 612 A, Eggeling 624, Esmans 662, Fanshawe 2519, Fiebrig-Gertz 685, Foxworthy 705, Garratt 744, Gleason 788 A, Gonggrijp 794, Groom 826, Hale 870, Harrar 906, Hédin 931, Heimsch 938, Howard 1088, Hummel 1109, Janssonius 1154, Jayawardana 1159, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Keen 1229, Koehler 1261, 1262, 1263, Kribs 1283, 1285, Lecomte 1333, 1334, Ledoux 1337, 1338, Louis 1393, Martin-Levigne 1450, Mell 1485, Méniard 1491, Meyer 1506, Normand 1608, Panshin 1649, 1650, Pearson and Brown 1679, Pereira 1687, Pfeiffer J. Ph. 1713, Piccioli 1716, Record 1776, 1780, 1781, 1782, 1783, 1784, 1787, 1801, 1809, 1818, 1825, 1839, 1843, 1851, 1880, Record and Hess 1886, 1891, Record and Mell 1894, Rendle 1918, Riera 1937, Scott 2075, 2076, Sim 2099, Spiekerkoetter 2168, Staner 2183, Stone 2202, 2203, 2206, 2207, Sudworth 2219, Swain 2224, Tang 2231, Torres 2269, Watt 2370, Welch 2396, Williams 2428, 2430, Yamabayashi 2478.

88. DICHAPETALACEAE

(FIG. 80 on p. 350; FIG. 82 on p. 360)

(Description of the leaf and young stem based mainly on those given respectively by Solereder and Engler and Krause (645).)

SUMMARY

(i) GENERAL

A tropical family of small trees and shrubs. Particularly noteworthy features include: the presence of unicellular **hairs** with conical or wart-shaped papillae on the surface; rubiaceous **stomata** confined to the lower surface of the leaf; the frequent occurrence of **mucilaginous cells** in the epidermis, hypodermis, and sometimes in the ground tissue of the petiole and branch.

(ii) WOOD

Vessels small, perforations simple or simple and scalariform, intervacular pitting usually alternate and minute, pits to ray cells similar, members of

medium length to moderately long. **Parenchyma** predominantly paratracheal, vasicentric to aliform, accompanied by varying amounts of diffuse parenchyma. **Rays** up to 5-6, occasionally 8-10, cells wide, markedly heterogeneous and often with sheath cells. **Fibres** with numerous, very small, bordered pits; of medium length.

LEAF

Usually dorsiventral. Simple, unicellular **hairs** with conical or wart-like papillae recorded in species of *Dichapetalum* and *Tapura* (Fig. 80 c). **Epidermis** consisting of 1 or several layers of cells. **Hypodermis** also recorded in species of *Dichapetalum*, *Stephanopodium*, *Tapura*. **Stomata** confined to the lower surface; rubiaceous in species of *Dichapetalum* and *Tapura* (Fig. 80 c). **Mesophyll** often partly composed of short palisade cells; spongy tissue absent from *Dichapetalum cymosum* (Hook.) Engl. Vascular bundles of the smaller **veins** accompanied by sclerenchyma in species of *Dichapetalum* and *Tapura*, branches of the sclerenchymatous elements sometimes extending into the mesophyll. **Mucilage cells** recorded in the epidermis, hypodermis, and sometimes in the ground tissue of the petiole, especially in certain species of *Stephanopodium* and *Tapura*. **Secretory cells** with brown contents also reported to occur in the mesophyll.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis. **Phelloderm** frequently sclerotic. Primary **cortex** often containing stone cells; mucilaginous cells recorded in the same region and in the ground tissue generally in species of *Stephanopodium* and *Tapura*. **Pericycle** including isolated groups of fibres. Secondary **phloem** containing sclerenchyma in certain species of *Stephanopodium*. **Xylem** including narrow vessels usually with simple perforations but occasionally (*Tapura guianensis* Aubl.) with scalariform perforation plates; fibres with bordered pits; rays of 2 distinct sizes, the smaller 1-4 and the larger up to 10 cells wide.

WOOD (Fig. 82 A-D)

Vessels usually moderately small (50-100 μ mean tangential diameter) but sometimes larger; solitary and in multiples of 2 or 3 cells and sometimes, according to Heimsch (938), in clusters and pore chains in *Gonypetalum* and *Tapura*; about 40 per sq. mm. in the material examined. Perforation plates simple in *Dichapetalum*, simple and scalariform, with up to 10 or more bars, in most species of *Tapura* (simple in the other species). Intervascular pitting typically alternate and minute and pits to ray cells similar, but Heimsch notes scalariform and transitional intervacular pitting in *Tapura obovata* Britton et P. Wils. and Record and Hess (1886) refer to occasional unilaterally compound pitting to ray cells. Tyloses reported by Heimsch in one species of *Dichapetalum*. Mean length 0.6-0.9 mm. **Parenchyma** typically predominantly paratracheal, about the vessels and as short, irregular wings, but always with some diffuse parenchyma in addition. Heimsch (938) notes more abundant apotracheal parenchyma (scattered cells to narrow bands) in *Tapura cubensis* (Poepp. et Endl.) Griseb. A specimen of *Tapura guianensis* Aubl. is

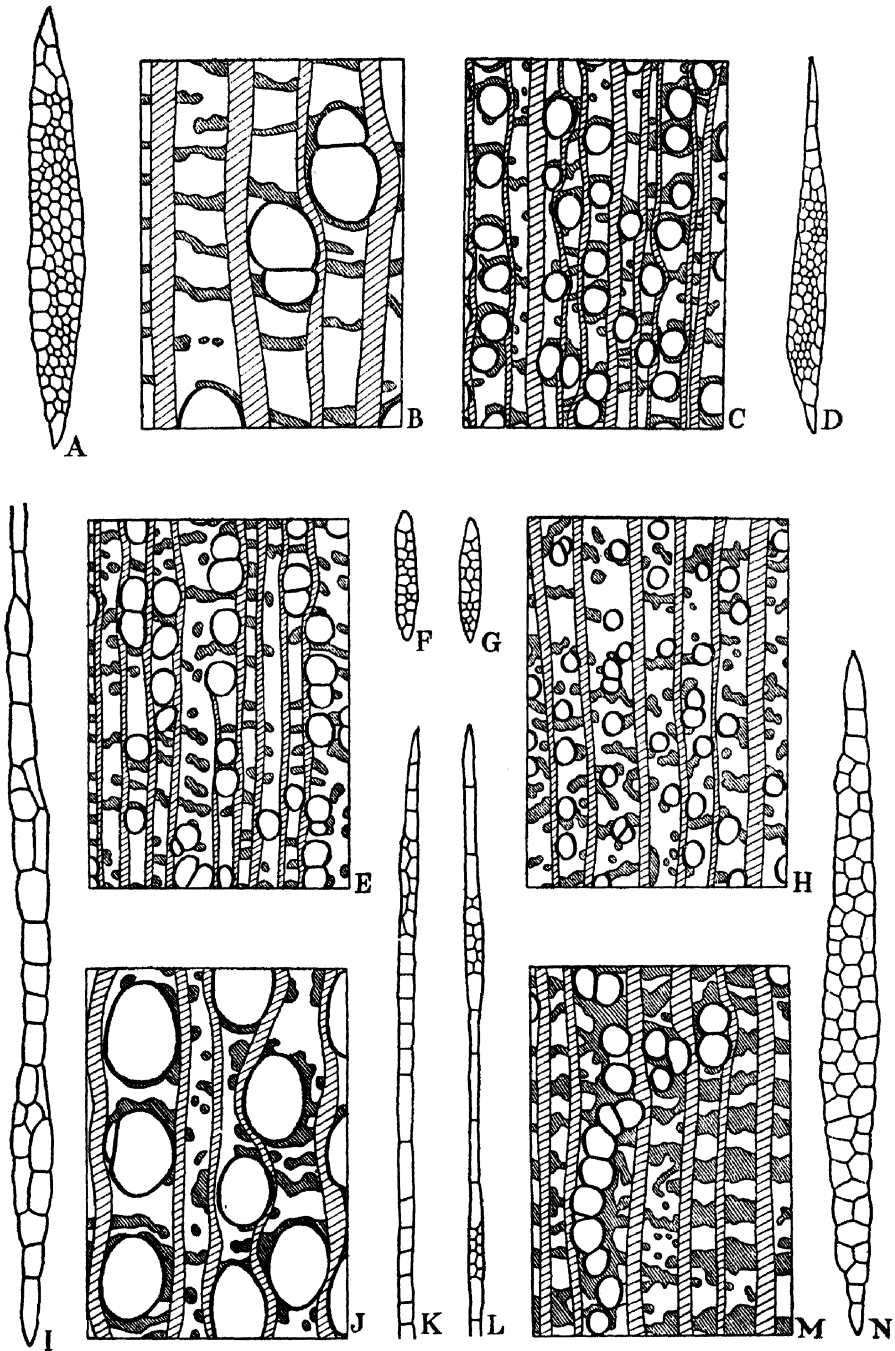


FIG. 82. *DICHAPE TALACEAE*, A-D; *OLACACEAE*, E-N

A, *Chaillietia gelonioides* Hook. f. B, *Chaillietia gelonioides* Hook. f. C, *Dichapetalum* sp. D, *Dichapetalum* sp. E, *Strombosia javanica* Bl. F, *Schoepfia schreberi* Gmel. G, *Ximenia americana* Linn. H, *Liriosma gracilis* A. C. Smith. I, *Aptandra zenkeri* Engl. J, *Ongokea klaineana* Pierre. K, *Strombosia javanica* Bl. L, *Ochanostachys amentacea* Mast. M, *Olax subscorpioides* Oliv. N, *Liriosma gracilis* A. C. Smith.

described by Williams as having numerous fine metatracheal bands, but differs in this respect and some others from material of this species examined by the author. Strands commonly of up to 8 cells. **Rays** usually up to 5 or 6 cells wide, sometimes up to 8–10 cells wide in *Dichapetalum* (938); more than 1 mm. high in some species; uniseriate numerous and composed entirely of square and upright cells; about 11 rays per mm.; heterogeneous (Kribs's Types I and II A), with 2 or 3 to several marginal rows of square and upright cells; sheath cells usually present. Solitary crystals often present in both upright and procumbent cells. **Fibres** with moderately to very numerous small pits on both radial and tangential walls, the pits with small borders; Heimsch (938) describes these cells as fibre-tracheids and tracheids. Walls moderately to very thick, occasionally gelatinous. Mean length about 1.5 mm.

The wood of a single specimen of *Chaillietia gelonoides* Hook. f. differs in many respects from the rest of the family, particularly in having numerous, bi-seriate apotracheal bands of parenchyma, shorter vessel members ($0.35\ \mu$), the smaller rays and parenchyma storied, and numerous fusiform parenchyma cells.

TAXONOMIC NOTES

The affinities of the Dichapetalaceae are not well established, and the few anatomical facts which have been recorded about the leaf and young stem are insufficient to be of much assistance in determining its taxonomic position.

On the basis of wood structure, Tippo (2261) places the family at about the same level of anatomical specialization as or slightly higher than the Cunoniaceae and Brunelliaceae. The material examined by the author, however, appears to be at a distinctly higher level than many of the genera in the Cunoniaceae.

Heimsch (938) suggests that the linking of this family with the Malpighiaceae, Vochysiaceae, Tremandraceae, Polygalaceae, and Trigonaceae, as in the systems of Hallier and Engler and Prantl, is preferable to linking it with either the Euphorbiaceae or Rosaceae as suggested by Wettstein and Hutchinson respectively.

ECONOMIC USES

The poisonous seeds of *Dichapetalum toxicarium* Baill. are used in West Africa for destroying rats.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

(Chaillietia), Dichapetalum, Stephanopodium, Tapura.

(ii) FOR WOOD STRUCTURE

Chaillietia, Dichapetalum, (Gonypetalum), Tapura.

LITERATURE

(i) On General Anatomy

Engler and Krause 645.

(ii) On Wood Structure

Heimsch 938, Record 1810, 1843, 1851, Record and Hess 1886, Tippo 2261, Tupper 2295, Williams 2430.

89. OLACACEAE

(As understood by Sleumer (2129))

(FIG. 82 on p. 360)

SUMMARY

(i) GENERAL

A tropical and sub-tropical family of trees, shrubs, and climbers. Anatomical characters which are common to the whole family appear to be lacking, except in so far as solitary and/or clustered **crystals** are generally present. The more interesting features include the following. (i) The presence of partially or wholly **silicified cells**, solitary or in groups, which occur in the mesophyll of certain genera (see list under 'Leaf' below). (ii) **Schizogenous secretory cavities** with resinous contents in the leaf and in the cortex of the axis in the Couleae (but not in other genera). (iii) **Laticiferous tubes**, which are usually branched and non-septate, in the primary cortex, phloem, pith, and sometimes in the leaf as well in the Couleae and *Heisteria*. The laticiferous tubes are, however, not accompanied by resinous cavities in *Heisteria*, although, as mentioned above, these occur in the Couleae. (iv) **Spicular fibres** (sometimes described as idioblasts) are to be found in the mesophyll of a number of genera.

(ii) WOOD

Vessels typically small, occasionally medium-sized; exclusively solitary or with numerous radial multiples; with a tendency to a radial or oblique pattern. Perforations exclusively scalariform or simple, with perforations to ray cells in many genera, intervacular pitting scalariform, opposite or alternate, the latter often very small; always with some large simple pits to ray and parenchyma cells; members very long in the genera with scalariform perforation plates, others of medium length to moderately short. **Parenchyma** typically apotracheal, diffuse to uniseriate, metatracheal bands; in *Schoepfia*, exclusively of paratracheal, storied fusiform cells. **Rays** 1-4 cells wide and usually 1.5-4 mm. high. The genera fall into two groups, (1) with 1-4 marginal rows of upright cells and a continuous multiseriate part composed of almost square cells that are rounded in tangential section and with intercellular spaces, and (2) with 10 or more marginal rows of upright cells, the middle part of the rays composed of alternating layers of upright and truly procumbent cells, the latter angular in tangential section and without intercellular spaces. **Fibres** with few or numerous distinctly bordered pits, rarely septate, moderately to very long in woods with scalariform perforation plates, of medium length in the others. **Vasicentric tracheids** present in *Olex*.

LEAF

Usually dorsiventral, but centric structure recorded in *Olex stricta* R. Br. and *Ximenia coriacea* Engl. **Hairs** mostly simple, but dendritic types present in the Couleae. Lower **epidermis** papillose in *Liriosma* and many species of *Olex*. **Stomata** confined to the lower surface in *Miquartia* and *Ochano-stachys*, present on both surfaces in certain species of *Olex* and in *Ximenia*; rubiaceous stomata recorded in *Coula* and in one species of *Olex*, but not in

other members of the last genus. **Hypoderm** below the upper epidermis recorded in *Cathedra* and in certain species of *Schoepfia*. Partly or wholly silicified cells, solitary or in groups, occur in the **mesophyll** of *Cathedra*, *Olax*, *Schoepfia*, and *Ximenia*.

Spicular cells (also described as sclerenchymatous fibres or idioblasts) occur in the mesophyll of *Eganthus*, *Endusa*, *Heisteria*, *Minquartia*, *Ochanostachys*, and *Scorodocarpus*. Terminal tracheids of the **veins** strongly developed in *Phlebocalymna*, *Schoepfia*, and *Ximenia*. Three bundles enter the base of the leaf in *Coula*, *Minquartia*, *Ochanostachys*, *Olax*, *Schoepfia*, and *Strombosia*, but transverse sections through the distal end of the **petiole** exhibit a solitary vascular strand in certain species of *Heisteria*, *Ochanostachys*, *Scorodocarpus*, and *Strombosia*, or an arc of separate bundles in species of *Liriosma*, *Olax*, and *Ximenia*. **Schizogenous secretory cavities** (see also 'Axis') with resinous contents (becoming blue when treated with eau de javelle) in the mesophyll of *Coula*, *Eganthus*, *Endusa*, *Minquartia*, and *Ochanostachys*, i.e. in all genera of the Couleae. Mesophyll cells sometimes containing drops of **resin** in *Cathedra*, *Schoepfia*, and *Ximenia*. **Laticiferous tubes** (see also 'Axis'), stated to be branched and non-septate, accompany the veins of *Heisteria*, *Minquartia*, and *Ochanostachys*. Similar elements lie free in the mesophyll of *Heisteria*, being recognizable with a lens as a network of transparent lines in the leaf. Similar but articulated tubes accompany the veins and also lie freely in the mesophyll of *Endusa*.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis, mostly composed of thin-walled cells, but intermixed with some having strongly thickened tangential walls in *Coula*, *Minquartia*, *Ochanostachys*. **Pericycle** containing a ring of sclerenchyma, usually composite and continuous, in *Heisteria*, *Minquartia*, *Ochanostachys*, certain species of *Scorodocarpus*, and in *Strombosia*; with bands or isolated strands of fibres in *Liriosma*, *Olax*, *Schoepfia*, and *Ximenia*. Secondary **phloem** partly sclerenchymatous in *Liriosma*. Vessels with simple and/or scalariform perforations. **Schizogenous secretory cavities** with resinous contents, similar to those described above under 'Leaf', occur in the cortex of *Coula*, *Minquartia*, and *Ochanostachys*. Branched, non-septate **laticiferous tubes**, present in the primary cortex, phloem, and pith of *Coula*, *Eganthus*, *Heisteria*, *Minquartia*, and *Ochanostachys*.

WOOD (Fig. 82 E-N)

Vessels typically small (less than $100\ \mu$ mean tangential diameter), medium-sized ($100\text{--}200\ \mu$) in at least some species of *Anacolosa*, *Chaunochiton*, *Coula*, *Ongokea*, and *Scorodocarpus*, very small ($25\text{--}50\ \mu$) in *Aptandra*, *Heisteria*, *Liriosma*, *Ptychopetalum*, and *Ximenia* p.p.; almost exclusively solitary in *Agonandra* (1886), *Heisteria*, *Liriosma*, *Ongokea*, *Phlebocalymna*, and sometimes in *Ximenia*, radial groups and multiples abundant in the other genera except *Liriosma*, and many species with a radial or oblique pattern, due to the radial multiples or to the grouping of solitary vessels and multiples, the pattern very distinct in *Olax* (Fig. 82 M) and rather vague in *Anacolosa*, *Aptandra*, *Coula*, *Endusa*, *Minquartia*, *Ochanostachys* p.p., *Ptychopetalum*, and

Strombosia; sometimes with a tendency to an oblique tangential pattern in *Schoepfia*; very variable in number in different genera, fewest (less than 5 per sq. mm.) in *Aptandra*, *Chaunochiton*, and *Ongokea*, most numerous (40–60 per sq. mm.) in *Heisteria* and *Ximenia*; diffuse-porous. Perforation plates scalariform in *Coula*, *Endusa*, *Heisteria*, *Minquartia*, *Ochanostachys*, *Scorodocarpus*, *Strombosia*, and *Strombosiopsis*, usually with moderately large perforations and few (6–10) bars, but with more than 20 bars in *Heisteria*. Chalk and Chatterway (358) have drawn attention to the common occurrence in this family of perforations between vessels and ray cells, whereby a vessel may pass through a ray and emerge on the other side, particularly in *Ptychopetalum anceps* Oliv. and *Strombosia javanica* Blume. It has been observed that, in addition to the type of perforated ray cells referred to in the above publication, the ray and parenchyma cells of *Chaunochiton*, *Ongokea*, and *Schoepfia*, where they adjoin vessels, often have what appear to be small round perforations in their walls; there is, however, no evidence that the vessels pass right through these rays, a fact that may possibly be explained by the different character of the rays in these genera. Solereder records a similar feature in *Cathedra rubricaulis* Miers. In *Ongokea* the contents of a ray cell can sometimes be observed protruding into the vessel through such a 'perforation', having the appearance of a minute tylosis. Intervascular pitting scalariform or opposite in *Heisteria*, *Strombosia*, and *Strombosiopsis*, opposite in *Coula* and *Scorodocarpus*, alternate in the remainder; pits small in *Anacolosa*, *Olax*, *Ongokea*, *Phlebocalymna*, *Ptychopetalum*, *Schoepfia*, and *Ximenia*; some of the pits to rays or parenchyma cells large, often simple, more rarely unilaterally compound, sometimes numerous, but rather rare in *Ongokea* and *Schoepfia*. Tyloses present in some species of *Minquartia*, *Ochanostachys*, *Scorodocarpus*, *Strombosia*, *Strombosiopsis*, and *Ximenia*, sometimes sclerosed in *Strombosiopsis tetrandra* Engl.; sometimes with gum-like deposits. Mean member length about 1.3–1.5 mm. in the genera with scalariform perforation plates, e.g. *Coula*, *Heisteria*, *Ochanostachys*, and *Strombosia*; about 0.3–0.5 in the genera with simple perforations, e.g. *Aptandra*, *Olax*, and *Ongokea*. **Parenchyma** typically apotracheal, varying from scattered cells in *Strombosia* (Fig. 82 E) and *Ximenia* to numerous, irregular, uniseriate bands forming a reticulate pattern with the rays, the bands more regular and biseriate in *Olax* (Fig. 82 M); with a few cells round the vessels (paratracheal) in addition to diffuse parenchyma in *Ongokea* (Fig. 82 J) and, according to Janssonius (1154), in *Anacolosa*. Chambered crystalliferous cells common in *Anacolosa*, *Aptandra*, *Chaunochiton*, *Coula*, *Endusa*, *Liriosma*, *Minquartia*, *Ochanostachys*, *Olax*, *Ongokea*, and *Ptychopetalum*; gum-like deposits present in a few species. Strands usually of 8 or more cells and sometimes up to 16, e.g. in *Strombosia*, but commonly of only 4 cells in *Aptandra*, *Chaunochiton*, *Liriosma*, *Olax*, *Ongokea*, and *Ximenia*. In *Schoepfia* the parenchyma is aliform and confluent, consists almost entirely of fusiform cells and is storied. **Rays**. The genera, other than *Schoepfia*, can be divided into two groups according to their ray characters. (1) *Aptandra*, *Chaunochiton*, *Liriosma* (Fig. 82 N), *Olax*, *Ongokea*, and *Phlebocalymna*: rays usually 2–3 cells wide, but up to 9 cells in *Phlebocalymna* and almost exclusively uniseriate in *Aptandra* (Fig. 82 I); 8–14 per mm.; cells large, rounded in tangential section, and with intercellular spaces; heterogeneous (Kribs's Type II A), with 1–4 marginal rows of uniseriate upright

cells, the multiseriate portions forming the bulk of the ray and composed of cells that are almost square in radial section and not very distinct from the upright cells in tangential section; uniseriates moderately numerous, composed of cells similar to those of the multiseriate rays; seldom more than 0.6 mm. in height in *Ongokea*, up to 2-3 mm. in the other genera; crystals abundant in chambered cells in *Ongokea*, not observed in the other genera. (2) *Anacolosa*, *Coula*, *Endusa*, *Minquartia*, *Ochanostachys* (Fig. 82 L), *Scorodocarpus*, *Strombosia* (Fig. 82 K), *Strombosiopsis*, and *Ximenia*: rays 2-4 cells wide, uniseriate in *Anacolosa*, *Ptychopetalum*, and *Strombosia javanica* Bl.; 12-20 per mm.; cells angular in tangential section and without intercellular spaces; markedly heterogeneous (Kribs's Type I), except in *Ximenia* (Type II B), with 10 or many more marginal rows of uniseriate upright cells, which are very high axially and narrow tangentially and radially, and are very distinct on tangential sections from the procumbent cells; the latter truly procumbent and occurring commonly in small groups alternating with rows of upright cells; the distribution and shape of the upright cells are sometimes very suggestive of tile cells. Uniseriates numerous, composed of square to upright cells. Crystals in chambered or ordinary cells present in most of the genera, abundant in *Endusa*, and gum-like deposits not uncommon; seldom more than 0.6 mm. in height in *Ximenia*, up to 2-5 mm. in the other genera. The rays of *Heisteria* and *Ptychopetalum* (uniseriate) are intermediate in character, the inner cells of the rays being comparable to the almost square multiseriate cells of group (1), but with many marginal rows of upright cells comparable to those of group (2). In *Schoepfia* (Fig. 82 F) the rays are up to 4 cells wide, short (seldom more than 15 cells and 250 μ high), with numerous rays only 1-3 cells high, 8-10 per mm., homogeneous (Kribs's Type I). **Fibres** with distinct and numerous bordered pits in *Heisteria*, *Liriosma*, *Ongokea*, *Phlebocalymna*, and *Ximenia*, the other genera with rather few, simple pits mainly limited to the walls in contact with ray or parenchyma cells, with funnel-shaped canals and slit-like inner and rounded outer apertures. With occasional septa in *Strombosia*. Walls usually very thick and often showing distinct zones. **Vascular tracheids** present in *Olax*. Mean length about 1.9-2.5 mm. in woods with scalariform perforation plates, e.g. *Coula*, *Heisteria*, *Ochanostachys*, and *Strombosia*; 1.0-1.8 mm. in woods with simple perforations, e.g. *Aptandra*, *Olax*, and *Ongokea*.

ROOT

Particulars concerning the anatomy of *Liriosma* root have been published by Youngken (2493).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Olacaceae, in combination with the Icacinaceae, constituted the Olacineae as understood in the system of Bentham and Hooker. The Olacaceae are here treated as a distinct family as understood by Sleumer (2129). The anatomical evidence at present available is not sufficiently comprehensive to give any clear indication of how closely related the Olacaceae and Icacinaceae may be, but this subject is discussed more fully below under Icacinaceae.

(ii) FROM WOOD STRUCTURE

The sub-family Schoepfioideae (with only one genus, *Schoepfia*) differs very considerably from the rest of the family, e.g. paratracheal parenchyma composed of fusiform cells, and short homogeneous rays, such differences being more marked and more numerous than the differences between many families. It has, however, in common with some of the other genera, the curious 'perforations' between the vessels and ray or wood parenchyma cells. It is more highly specialized than the other genera of the family and some of the differences may be due to this.

The family, even if *Schoepfia* is excluded, is by no means uniform in structure, but though separate groups of genera can be distinguished by single characters, such as radial grouping of vessels, solitary vessels, fibre-tracheids, &c., these groups overlap and have more points of resemblance to than differences from the remaining genera. The family includes genera at very different levels of specialization and specialization may have taken place very unevenly in different elements, e.g. advanced vessel pitting may be accompanied by a primitive type of ray.

'Ray Type 1' includes all the genera examined of Sleumer's Olacoideae, i.e. *Aptandra*, *Liriosma*, *Olax*, and *Ongokea*, except for *Ptychopetalum*, which has uniseriate rays of intermediate type, but this group also includes *Chaunochiton* of the Discalacoideae. 'Ray Type 2', on the other hand, includes all the genera examined of the Discalacoideae, i.e. *Anacolosa*, *Coula*, *Endusa*, *Minquartia*, *Ochanostachys*, *Scorodocarpus*, *Strombosia*, *Strombosiopsis*, and *Ximenia*, except for *Heisteria*, which is intermediate in character, and *Chaunochiton*. A similar difference in type of ray occurs in the Octoknemaceae, between *Octoknema borealis* Hutch. et J. M. Dalz. and *Okoubaka aubrevillei* Pellegrin et D. Normand (p. 378).

ECONOMIC USES

The kernels of the Coula or Gaboon nut (*Coula edulis* Baill.) are edible after cooking, and the fruits and sometimes the kernels of the Wild Olive (*Ximenia americana* L.) are also eaten, although their value has been much disputed. The woods are of little commercial importance owing to small dimensions or quantities, though some are of good quality. Black Manwood, *Minquartia* sp., is highly valued in Central America for its durability and has been used for railway sleepers, posts, and poles. The wood of *Ximenia americana* Linn. is sometimes used as a substitute for sandalwood (Metcalfe, 1497).

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Cathedra, *Coula*, *Eganthus*, *Endusa*, *Heisteria*, *Liriosma*, *Minquartia*, *Ochanostachys*, *Olax*, *Phlebocalymna*, *Schoepfia*, *Scorodocarpus*, *Strombosia*, *Ximenia*.

(ii) FOR WOOD STRUCTURE

(*Agonandra*), *Anacolosa*, *Aptandra*, *Chaunochiton*, *Coula*, *Endusa*, *Heisteria*, *Liriosma*, *Minquartia*, *Ochanostachys*, *Olax*, *Ongokea*, *Phlebocalymna*, *Ptychopetalum*, *Schoepfia*, *Scorodocarpus*, *Strombosia*, *Strombosiopsis*, and *Ximenia*.

LITERATURE

(i) *On General Anatomy*

Sleumer 2129, Youngken 2493.

(ii) *On Wood Structure*

Baker 104, Benoist 170, den Berger 179, 182, 183, Besson 186, Burgerstein 312, Chalk and Chattaway 358, Cooper 461, Foxworthy 705, Howard 1088, Janssonius 1154, Jentsch 1178, Metcalfe 1497, Normand 1619, Pfeiffer, J. Ph. 1713, Record 1843, 1851, 1853, Record and Hess 1886, Record and Mell 1894, Williams 2426.

90. ICACINACEAE

(FIG. 84 on p. 368; FIG. 85 on p. 370; FIG. 86 on p. 372; FIG. 88 on p. 382)

SUMMARY

(i) GENERAL

A tropical family of woody plants including erect trees and shrubs as well as climbers. The general anatomy of the family is still imperfectly known, in spite of the fact that it was subdivided into tribes by Engler (629, 630), many years ago on an anatomical basis. The characters employed included the presence or absence of scalariform perforation plates to the vessels, as well as of interxylary phloem, together with variations in the equal or unequal development of xylem around the periphery of the stem. Recent work of Bailey and Howard (81) has shown this classification to be unreliable (see also under 'Taxonomic and Phylogenetic Notes' on p. 375). There have also been considerable differences of opinion concerning the taxonomy and nomenclature of the family, both of which facts make it difficult to interpret such anatomical facts as have been recorded in the literature. The phylogenetic conclusions drawn from the anatomical work by Bailey and Howard have aroused much interest in recent years. **Anomalous structure** occurs in certain genera.

(ii) Wood

Vessels showing an unusual range from unspecialized to specialized forms; the former typically numerous, small, solitary, with exclusively scalariform perforation plates, scalariform or opposite pitting and very long members, the latter small to medium-sized, often in radial multiples, and irregular groups, and occasionally with a radial or tangential pattern, with simple perforations, alternate pitting and members of medium length. Pits to ray cells or parenchyma usually similar to the intervacular pitting, occasionally larger. **Parenchyma** apotracheal in the genera with exclusively scalariform perforation plates, mostly diffuse, but sometimes in definite bands; in the more advanced woods varying from banded apotracheal with a little vasicentric to predominantly paratracheal—usually vasicentric where sparse and aliform where more abundant. **Rays** very commonly of 2 distinct sizes, the larger rays from 3 to 10 or more cells wide, heterogeneous and often with sheath cells; the large rays exhibiting varying stages of dissection into smaller units and 'aggregate' in some species. **Fibres** typically with bordered pits, often large and conspicuous, with simple pits in 2 genera; varying from very long in the unspecialized to medium length in the more highly specialized genera.

Included phloem of various types present in the tribes of climbing plants; with included phloem in the Sarcostigmateae.

LEAF

Hairs simple, unicellular of varied length not uncommon in *Apodytes*,

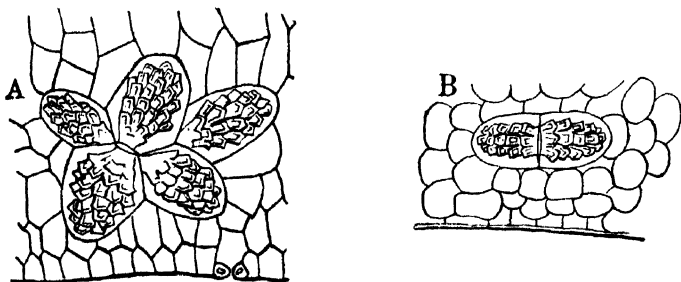


FIG. 83. OPILIACEAE

A-B, A group and a pair of cystoliths from the mesophyll of *Cansjera timorensis* Decne.—After Van Tieghem.

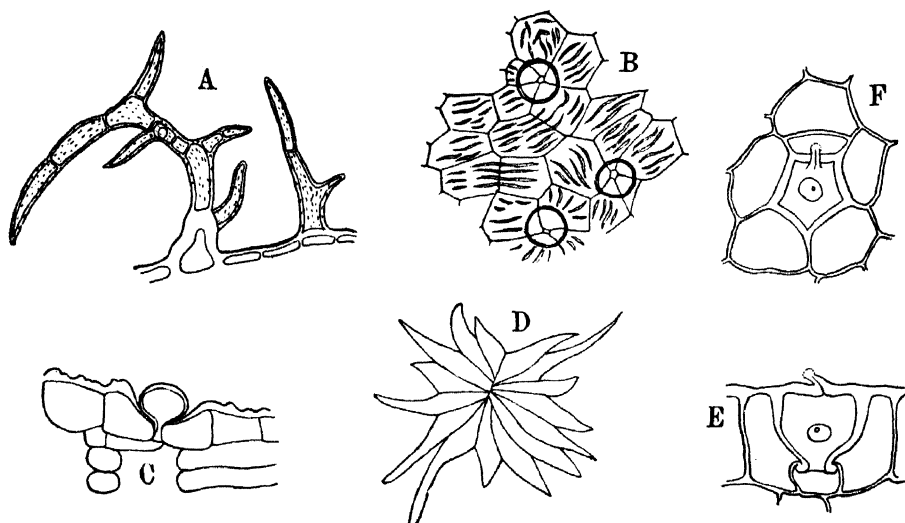


FIG. 84. OPILIACEAE, A; ICACINACEAE, B-F

Hairs of: A, *Cansjera parvifolia* Kurz; B-D, *Platea excelsa* Bl.; E-F, Hydathodes of *Gonocaryum pyriforme* Scheff.—A-D by Solereder, E-F after Haberlandt.

Discophora, *Emmotum*, *Liriosma*, *Mappia*, *Poraqueiba*. Spherical unicellular hairs and multicellular, peltate hairs also recorded in *Platea excelsa* Bl. (Fig. 84 B-D). Tufted hairs in *Phytocrene bracteata* Wall. Unicellular bladder-like hairs recorded in *Cardiopteris rumphii* H. Baill. Cells of the **epidermis** sometimes mucilaginous in *Apodytes* and *Mappia*. Lower epidermis papillose in *Apodytes dimidiata* E. Mey. **Stomata** ranunculaceous to cruciferous in a few species of *Alsodeiopsis*, *Lasianthera*, *Stemonurus*, rubiaceous in *Apodytes dimidiata* E. Mey. **Hydathodes** recorded in *Gonocaryum pyriforme* Scheff. (Fig. 84 E-F) and small ovoid bodies at the ends of the veins serving for water

secretion in *Pyrenacantha malvaefolia* Eng., *P. scandens* Harv., and *Trematosperma cordatum* Urb. **Mesophyll** containing sclerenchymatous fibres in *Desmostachys renschii* O. Hoffm. and *Discophora guianensis* Miers. Sclerenchymatous fibres in the veins of *Emmotum* provided with numerous, oblique, slit-shaped, spirally arranged pits giving the appearance of spiral thickening. **Petiole** of *Apodytes dimidiata* E. Mey. (Fig. 88 1) exhibiting an arc-shaped vascular strand in transverse sections through the distal end. Articulated **laticiferous tubes** recorded in the veins and petiole of *Cardiopteris lobata* Baill. Solitary **crystals** present in certain species of *Icacina*, *Mappia*, *Poraqueiba*, clustered crystals in species of *Apodytes*, *Citronella mucronata* (Ruiz. et Pav.) D. Don, *Desmostachys*, *Discophora*, *Emmotum*, *Poraqueiba*; crystal-sand in *Apodytes andamanica* Kurz.

AXIS

YOUNG STEM (Fig. 88 L-M)

Outer part of the **cortex** of the young stem containing well-developed stone cells in *Phytocrene macrophylla* Bl. **Cork** arising in the epidermis in species of *Apodytes*, *Iodes*, *Lasianthera*, *Pennantia*, *Phytocrene*, *Trematosperma*. Cork cells sometimes with strongly thickened, inner tangential walls in *Apodytes*, *Lasianthera*, *Pennantia*. **Pericycle** recorded by Solereder as having a composite and continuous ring of sclerenchyma in *Emmotum fagifolium* Desv., *Gonocaryum gracile* Miq., *Leptaulus daphnoides* Benth., *Pennantia endlicheri* Russ., *Platea excelsa* Bl., *Poraqueiba guianensis* Aubl., *Stemonurus javanicus* Bl., *Urandra apicalis* Thur., containing isolated bundles of fibres in *Cardiopteris*, or a loose ring of fibres in *Pyrenacantha volubilis* Hook. Young stem with a circle of unevenly distributed **vascular bundles** around the pith in *Phytocrene macrophylla* Bl. Inversely orientated **medullary bundles** stated to occur in *Iodes tomentilla* Miq. Howard (1096, 1097), writing of the **xylem** of *Codiocarpus*, *Discophora*, *Gastrolepis*, *Irvingbaileya*, *Lasianthera*, *Medusanthra* as represented in twigs taken from herbarium sheets, states that all of these genera belonging to the Icacinaceae possess at least a proportion of vessel elements with scalariform perforation plates, or transitions between these and simple perforations. Further particulars concerning the individual genera are given as follows:

(i) *Discophora*. Vessels aggregated or clustered and provided with scalariform perforation plates, simple perforations, and transitional forms. Intervascular and vessel-parenchyma pits large, scattered, circular, alternate. Ground tissue of the wood consisting of fibre-tracheids with pits 3–5 μ in diameter. Wood parenchyma abundant, diffuse to semi-banded or scanty paratracheal. Rays heterogeneous, 1 to several cells wide; uniseriate tall, composed of high cells.

(ii) *Gastrolepis*. Vessels in loose clusters and provided with scalariform perforation plates as well as simple, and transitional perforations. Intervascular and vessel-parenchyma pits showing transitions from scalariform to bordered types. Ground tissue of the wood consisting of dense fibre-tracheids. Wood parenchyma tending to be scanty—paratracheal with vestiges of diffuse elements.

(iii) *Irvingbaileya*. Vessels more or less aggregated and provided with

scalariform perforation plates as well as simple, and transitional perforations. Intervascular and vessel-parenchyma pits tending to be scalariform-opposite. Ground tissue of wood consisting of tracheids with wide lumina. Wood parenchyma scanty—diffuse with little or no tendency to form bands.

(iv) *Lasianthera*. Vessels scattered or isolated. Vessel-parenchyma pits scalariform with enlarged apertures. Ground tissue of wood consisting of

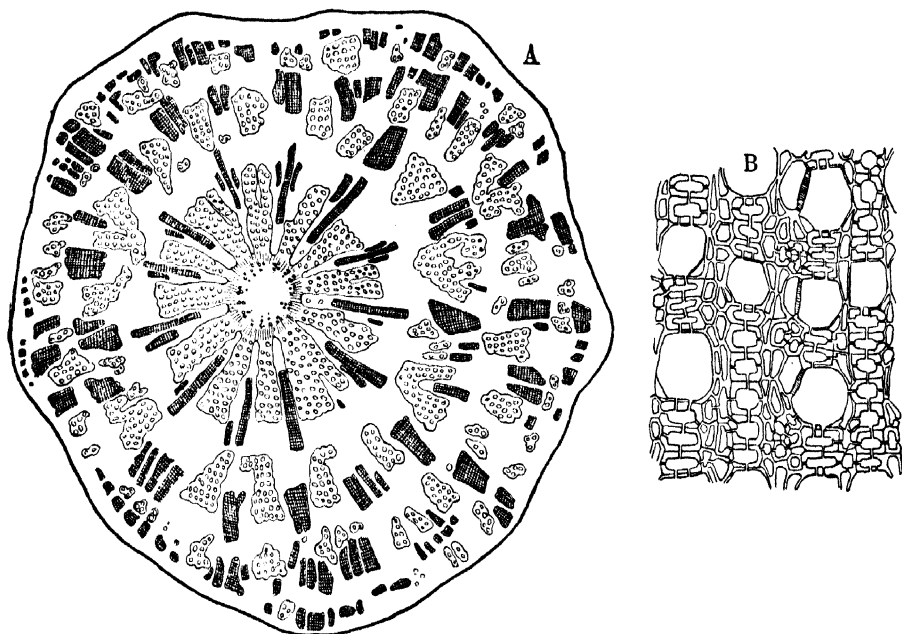


FIG. 85. ICACINACEAE

Phytocrene macrophylla Bl. A, Transverse section through the axis (magnification about 2:1). B, Transverse section through a piece of a xylem wedge.—After Robinson.

tracheids with inconspicuously bordered pits. Wood parenchyma scanty, diffuse, or abaxial-paratracheal.

(v) *Medusanthera*. Vessels arranged in irregular multiples; with a smaller proportion of scalariform perforation plates than in the related genera. Intervascular and vessel-parenchyma pits small; ground tissue of wood consisting of fibre-tracheids with minutely bordered pits, 2.0–2.5 μ in diameter. Rays similar to those of *Discophora*.

Bailey and Howard (81) describe a study of the nodal anatomy in which it was shown that amongst the Icacinioideae some of the genera possess trilacunar (primitive) nodes and others unilacunar (advanced) nodes. Even within the Icacinaceae there are genera in each of these categories, whilst in the Iodeae, Sarcostigmateae, and Phytocreneae, which are chiefly climbers, only unilacunar nodes were observed. Members of the last three tribes are climbing or twining in habit, whereas the trilacunar Icacinaceae are erect. These tribes are regarded as phylogenetically more advanced than the usually erect trilacunar Icacinaceae, whilst the unilacunar Icacinaceae are taken to represent a transitional stage between the trilacunar Icacinaceae and the other tribes.

These differences in phylogentic specialization are correlated with others described below under 'Wood', whilst further reference to the subject is made under 'Phylogenetic and Taxonomic Notes'.

Mucilage spaces recorded in the soft tissues of the stem of *Phytocrene macrophylla* Bl. The secretion in these spaces, when present, stated to be strongly fluorescent. **Mucilage canals** said to occur in *Trematosperma*, and lysigenous canals, arising secondarily on the inside of the vascular bundles of the axis, in *Cardiopteris*.

WOOD (Fig. 86 A-I)

Vessels small (less than $100\ \mu$ mean tangential diameter), just medium-sized in a few genera, very small (less than $50\ \mu$) in *Alsodeiopsis*, *Apodytes*, *Leptaulus*, *Medusanthera*, *Ottoschulzia*, and *Pennantia*. Exclusively solitary or nearly so in genera with exclusively scalariform perforation plates (except *Pittosporopsis* and *Platea*) and also in some species of *Cantleya*, *Gonocaryum*, *Lasianthera*, *Leptaulus*, and *Stemonurus*, in which the perforation plates are both scalariform and simple (82). Radial multiples common and sometimes of 4 or more cells in *Alsodeiopsis*, *Discophora*, *Mappia* (82), *Nothapodytes* (82), and *Platea* p.p., and with occasional irregular clusters in some of these woods; with a tangential pattern in *Desmostachys* (Fig. 86 G) and *Ottoschulzia*. Varying in number from about 6 to 80 per sq. mm., fewest (6-10 per sq. mm.) in *Alsodeiopsis*, *Cantleya*, *Medusanthera*, and *Platea*, most numerous (50 or more per sq. mm.) in *Leptaulus* and *Pennantia*. Spiral thickening reported by Record (1801) in *Citronella* (*Villaresia*) *mucronata* D. Don. According to Bailey and Howard (82) the perforation plates are (a) scalariform only in *Anisomallon*, *Apodytes*, *Calatola*, *Cassinopsis*, *Citronella*, *Dendrobangia*, *Emmotum*, *Oecopetalum*, *Ottoschulzia*, *Pennantia*, *Pittosporopsis*, *Platea*, and *Poraqueiba*,¹ (b) scalariform and simple in *Cantleya*, *Discophora*, *Gastrolepis*, *Gonocaryum*, *Grisollea*, *Leptaulus*, *Medusanthera*, *Stemonurus*, and *Urandra*, and (c) simple only in *Alsodeiopsis*, *Chlamydocarya*, *Desmostachys*, *Hosiea*, *Humirianthera*, *Icacina*, *Lavigeria*, *Leretia*, *Mappia*, *Mappianthus*, *Merrilliodendron*, *Miquelia*, *Natsiatum*, *Nothapodytes*, *Phytocrene*, *Pleurisanthes*, *Polycephalum*, *Polyporandra*, *Pyrenacantha*, *Rhaphiostylis*, *Rhyticaryum*, and *Sarcostigma*; scalariform perforation plates with thin and numerous bars (20-50) in *Anisomallon*, *Apodytes*, *Calatola*, *Citronella*, *Pennantia*, and *Platea*; the perforations commonly subdivided into reticulate patterns in *Calatola* and *Pennantia*. Intervascular pitting usually transitional between scalariform and opposite or opposite in woods in which scalariform perforation plates occur, and alternate where the perforations are simple, the pits very small in *Alsodeiopsis*, *Apodytes*, *Medusanthera*, and *Pennantia*, with striations due to coalescent apertures in *Alsodeiopsis* and *Desmostachys*; pits to ray and parenchyma cells usually similar to the intervacular pit-pairs, but enlarged and almost simple in *Discophora* and *Gonocaryum*. Tyloses sometimes present in *Cantleya* and *Emmotum*, thick-walled in the former. Bailey and Howard (83) give the following mean member lengths: Icacinaceae (a) Trilacunar, with scalariform perforation plates, 1.47 mm., (b) Trilacunar, with simple and scalariform perforation plates, 1.05 mm., (c) Unilacunar, 0.59 mm. For the

¹ Williams (2430) describes both simple and scalariform plates in *Poraqueiba sericea* Tul.

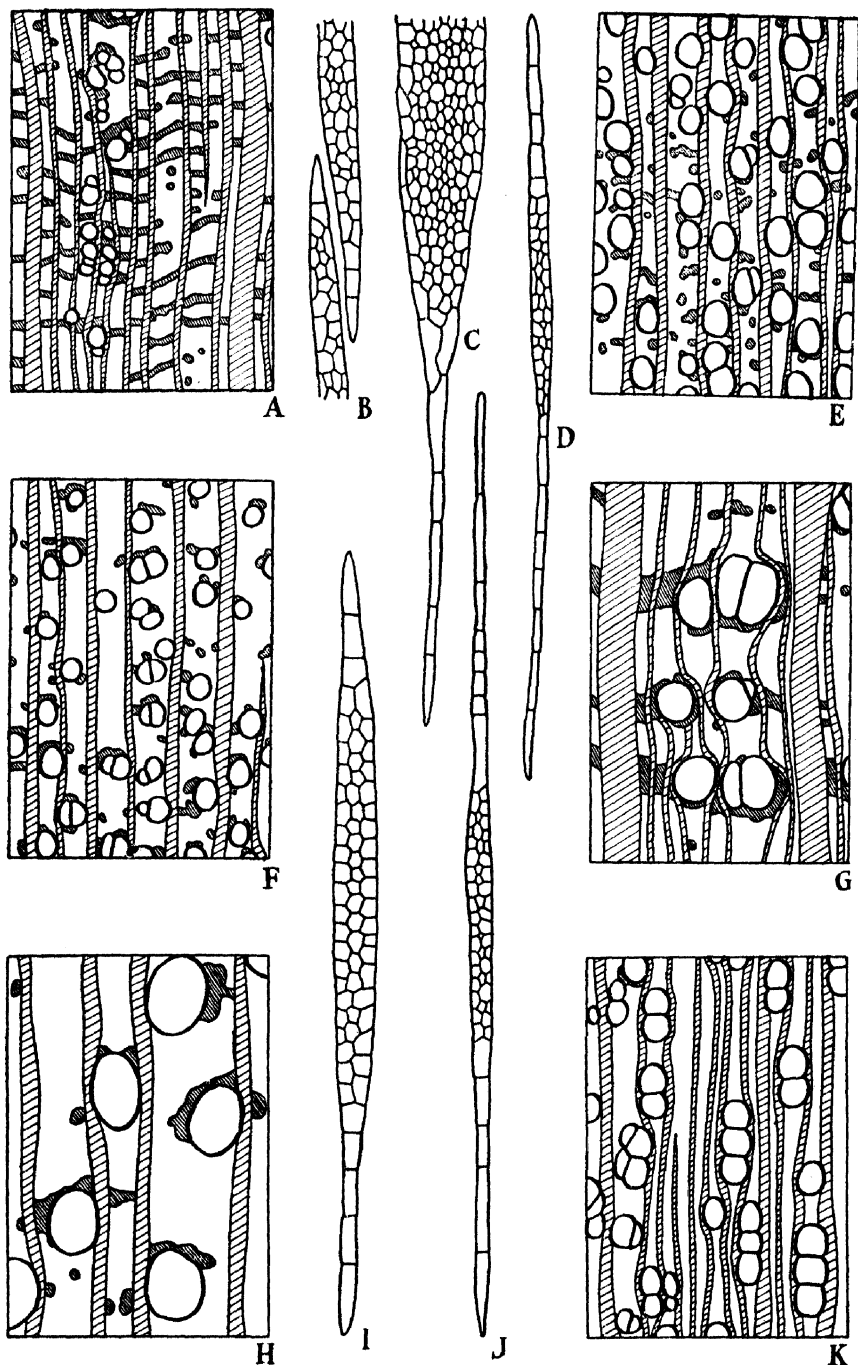


FIG. 86. ICACINACEAE, A-I; OCTOKNEMATACEAE, J, K

A, *Alsodeiopsis staudtii* Engl. B, *A. staudtii* Engl. C, *Pennantia cunninghamii* Miers. D, *Apodytes dimidiata* E. Mey. E, *A. dimidiata* E. Mey. F, *Leptaulus daphnoides* Benth. G, *Desmostachys vogelii* Stapf. H, *Cantleya corniculata* (Becc.) Howard. I, *C. corniculata* (Becc.) Howard. J, *Octoknema borealis* Hutch. et Dalz. K, *O. borealis* Hutch. et Dalz.

Iodeae, Sarcostigmateae, and Phytocreneae, 0.47 mm. **Parenchyma** varying considerably in type and amount and often unstable. Bailey and Howard (83) have shown that the type of parenchyma is closely related to the degree of specialization of the vessels. Woods with exclusively scalariform perforation plates typically with abundant apotracheal parenchyma in numerous short lines (Fig. 86 E), sometimes with a tendency to definite bands in *Ottoschulzia* and *Poraqueiba*, and with some vasicentric parenchyma in *Citronella* and *Emmotum*; of the woods with both simple and scalariform perforation plates, *Discophora* and *Stemonurus* have banded apotracheal parenchyma only, the others have at least some paratracheal parenchyma, as in *Gonocaryum* with diffuse and vasicentric, or predominantly paratracheal parenchyma (Fig. 86 II), e.g. aliform in *Cantleya* p.p. and *Stemonurus* or with a few cells round the vessels in *Cantleya* p.p. and *Gastrolepia* (83), and with short rows attached to the vessels on the abaxial surfaces in *Leptaulus* (Fig. 86 F); woods with exclusively simple perforations commonly with some or predominantly paratracheal parenchyma; with both apotracheal bands and paratracheal (vasicentric) parenchyma in *Alsodeiopsis* (Fig. 86 A), *Mappia*, *Medusanthera*, *Merrilliodendron*, and *Nothapodytes* (83); according to Bailey and Howard (83), in *Desmostachys* (Fig. 86 G) and the following genera with a scrambling or climbing habit of growth—*Humirianthera*, *Icacina*, *Lavigeria*, *Leretia*, *Pleurisanthes*, *Rhaphiostylis*, and *Rhyticaryum*—the banded apotracheal parenchyma is conspicuously reduced, giving varied transitions between banded apotracheal and paratracheal types of distribution and forms having a predominantly paratracheal or vasicentric distribution. These authors note similar unstable types in small-vesselled parts of the stem of certain representatives of the Phytocreneae and Iodeae, whereas in the large-vesselled anomalous wood of these plants the parenchyma tends to be more dominantly paratracheal; they also note that in *Sarcostigma*, and at times in certain of the Phytocreneae, the strands of wood parenchyma tend to be replaced by curious septate parenchymatous elements. Strands usually of 8 cells, sometimes more in the unspecialized genera. Crystals not observed. **Rays** very variable in width and height, varying from up to 3 or 4 cells wide in *Anisomallon*, *Apodytes*, *Cantleya*, *Discophora*, *Leptaulus*, and *Platea excelsa* Bl. up to 10 or more cells wide in *Alsodeiopsis schumannii* Engl., *Citronella*, *Emmotum*, *Medusanthera*, *Ottoschulzia*, *Pennantia*, *Poraqueiba*, and *Stemonurus*; varying in height from about 1 mm. in *Leptaulus* to 4 mm. or more; commonly of 2 distinct sizes, except where the multiseriate rays are narrow, as in *Apodytes* (Fig. 86 D), *Calatola*, *Cantleya*, and *Discophora*, or where uniseriate rays are very scarce, as in *Tylecarpus*; the large primary multiseriate rays commonly dissected into smaller units (Fig. 86 B) and producing typical 'aggregate' rays in some species of *Alsodeiopsis* and *Poraqueiba* (84); the uniseriate rays typically numerous, often very high and usually composed of very high upright cells, exceptionally high in *Desmostachys vogelii* Stapf. (84), least numerous in some species of *Cantleya*, *Citronella*, *Discophora*, *Gastrolepia*, *Gonocaryum*, and *Medusanthera*; varying in number from about 4 to 16 rays per mm., fewest in some species of *Cantleya*, *Citronella*, and *Medusanthera*; very distinctly heterogeneous (Kribs's Type I in the unspecialized genera, Type II A and B in the others), with several marginal rows of markedly upright cells, rows seldom exceeding 4 in *Cantleya*, *Citronella*, and *Medusanthera* and frequently

with 10 or more rows in *Anisomallon*, *Calatola*, *Ottoschulzia*, *Platea*, and *Stemonurus*; commonly with sheath cells. One or more crystals occur in the ordinary ray cells of several species and, less frequently, small quantities of dark-coloured deposits. According to Bailey and Howard (84) in the highly specialized climbing plants of the Iodeae, Sarcostigmateae, and Phytocreneae there is a conspicuous tendency for the elimination of multiseriate rays from the first-formed secondary xylem; multiseriate rays occur in some species of the Iodeae, either extending outwards from gaps in the primary body or arising abruptly at some distance from the stele; the first-formed secondary xylem of most species of *Iodes* and *Polyporandra* has multiseriate rays with or without varying numbers of biseriate or aggregate rays, a type of structure that predominates through relatively thick stems in the Sarcostigmateae; in the Iodeae much-modified multiseriate rays with very thin-walled cells are retained in the later-formed anomalous wood. In the Phytocreneae multiseriate rays are usually eliminated from young stems except for pairs of wide rays, which flank the inwardly projecting strands of phloem. **Fibres**, according to Bailey and Howard (83), with large conspicuous bordered pits in the genera with exclusively scalariform perforation plates and also in some species of *Cantleya*; in *Discophora*, *Gastrolepis*, *Gonocaryum*, *Grisollea*, *Lasianthera*, *Leptaulus*, and *Medusanthera* the pits are bordered, but the borders are smaller and the chambers flatter and less obvious in section; in the aborescent genera with exclusively simple perforations there is a conspicuous reduction in the size of the bordered pits (less marked in *Merrilliodendron*) and the pits are simple in *Mappia* and *Nothapodytes*. Walls usually thick, sometimes with extremely small lumina, but thin-walled in *Platea*. Bailey and Howard (83) give the following mean lengths: Icachineae (a) Trilacunar, with scalariform perforation plates, 2.49 mm., (b) Trilacunar with simple and scalariform perforation plates, 2.58 mm., (c) Unilacunar, 1.60 mm.; for the Iodeae, Sarcostigmateae, and Phytocreneae, 0.87 mm. Bailey and Howard (83) note that the sectional area of the fibres is much smaller in the members of the Icacinaceae with exclusively simple perforations. In the unilacunar Icacinaceae, having a scrambling or scandent habit of growth, as in the scandent Iodeae Sarcostigmateae and Phytocreneae, Bailey and Howard state that 'there are reversals in the specialization of the imperforate tracheary elements, which culminate in the formation of curious short tracheids. These tracheary cells are characterized by having relatively conspicuous lumina and numerous bordered pits. They are most typically developed in the large-vesselled anomalous wood of *Lavigeria*, *Pleurisanthes* and of various representatives of the Iodeae and Phytocreneae. Intermediate or transitional stages of their phylogenetic differentiation occur in *Humirianthera*, *Icacina*, *Leretia*, *Mappianthus*, *Rhaphiostylis*, and *Sarcostigma*, as well as in the denser, smaller-vesselled parts of the stems of certain Iodeae and Phytocreneae.' **Included (interxylary) phloem**. Bailey and Howard (81) refer to the occurrence of interxylary phloem in the climbing shrubs of the tribe Sarcostigmateae, and to various forms of anomalous structure in young stems in the Iodeae and Phytocreneae. For further particulars see next paragraph.

ANOMALOUS STRUCTURE

Tree trunks flanged in *Citronella moorei* (F. Muell.) Howard, according to

Francis (708). The xylem and secondary phloem of *Phytocrene* (Fig. 85 A-B) are differentiated as alternating wedges, the xylem ring consisting of well-developed teeth of wood with phloem patches between them. The normal phloem strands are also well developed but with weak areas of xylem between them. This abnormal structure is absent from young stems. Zones of growth, each exhibiting the abnormal type of structure described above, arise from successive cambia in certain species of *Chlamydocarya*, *Phytocrene*, and *Sarcostigma*. Each zone of growth either completely encircles the branch or is confined to certain segments, according to Pfeiffer (1712), Solereder, and Timmermans (2261). Alternating wedges of xylem and phloem also recorded in *Pyrenacantha*. **Interxylary phloem** present in *Chlamydocarya* and *Sarcostigma*. Instances where unequal increases in the thickness of the wood sometimes become obliterated in old material have been recorded in *Iodes* and *Natsiatum*. For other information concerning interxylary phloem see 'Wood'.

TAXONOMIC AND PHYLOGENETIC NOTES

Many of the genera of the Icacinaceae were included in the system of Bentham and Hooker in the tribes Icachineae and Phytocreneae of the Olacineae. In the system of Engler and Prantl the Icacinaceae are treated as a separate family under Sapindales. The Icacinaceae are also recognized as a separate family by Hutchinson, who, like Wettstein, places them in the Celastrales. When considering the relationship between the Icacinaceae and Olaceae, it is interesting to note the occurrence of articulated laticiferous tubes in *Cardiopteris* similar to those which are to be found in the tribe Couleae of the Olacaceae. Then again the presence of sclerenchymatous fibres in the mesophyll of *Desmostachys* and *Discophora* is reminiscent of those in *Eganthus*, *Endusa*, *Heisteria*, *Minquartia*, *Ochanostachys*, and *Scorodocarpus*.

It will be seen from the various references to the work of Bailey and Howard given above under the description of the axis that these authors have used the anatomical method to investigate the phylogenetic relationships within the family. Starting with the assumption, discussed on p. xxxix of this book, that the trilacunar node is more primitive than the unilacunar type, Bailey and Howard first showed that trilacunar nodes occur only in the Icachineae, whereas in certain other genera of the Icachineae, as well as in the Iodeae, Sarcostigmateae, and Phytocreneae, only unilacunar nodes were observed. These last three tribes, consisting mostly of twining or climbing plants, are therefore regarded as more specialized than the trilacunar Icachineae. The unilacunar Icachineae are taken to be intermediate between these two categories.

The same authors also examined the vessel members, wood fibres, wood parenchyma, and types of ray which occur in the family from the phylogenetic standpoint. In general there was found to be good agreement concerning the lines of specialization within the family no matter which of these characters is used as an indicator, but the evidence provided by the vessel elements and wood fibres seems more definite than that derived from the parenchyma or rays. For instance, when using the characters of the vessel members, the authors show how the Icacinoidae may be divided into three major categories: I. Those in which the vessel perforation plates are exclusively scalariform. II. Those in which a mixture of simple and scalariform perforation plates

occur. III. Those in which the perforations are exclusively simple. Genera with unilacunar (advanced) nodal structure were all found to be in group III with exclusively simple (advanced) perforations. Conversely, trilacunar nodes and scalariform perforation plates were found to occur together. Bailey and Howard suggest that these facts are of taxonomic as well as of phylogenetic significance. They wisely state, however, that 'Parallel developments and convergent evolution are of such common occurrence in foliar and cauline, as well as in floral structures that evidence from all parts of the plant must be harmonized and integrated in attempting to determine actual genetic affinities within an order, family, sub-family or tribe'. After describing and discussing the evidence from the wood fibres, rays, and parenchyma as well as that from the vessels, the same authors conclude that, although the trends of specialization in all of these organs tend to run parallel with one another, 'the rates of evolutionary modifications in one category of these tissue cells not infrequently are retarded or accelerated in relation to the changes that are occurring in the other tissue cells'. Bailey and Howard's researches have clearly demonstrated some most interesting correlations.

ECONOMIC USES

A substitute for Maté Tea (*Ilex paraguariensis* St. Hil.) is obtained from *Citronella gongonha* (Mart.) Howard (syn. *Villaresia gongonha* Miers), the substitute having a strong resemblance to the genuine article. The anatomical structure has been described by Lendner (1357). Starch and oil are obtained from the fruit and seed of *Poraqueiba* in the Para region of Brazil. *Humirianthera* is cultivated for the sake of its fleshy tubers and root-stocks, but the starchy material must be washed before use as it is otherwise toxic. A blue dye is obtained from the bark, leaves, and fruits of *Calatola*. The woods of this family are of little commercial importance. That of *Apodytes dimidiata* E. Mey. is used in South Africa for cart and wagon felloes and Record and Hess (1886) note species of *Dendrobangia* and *Ottoschulzia* as being used locally in tropical America and the West Indies.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Alsodeiopsis, Apodytes, Cardiopteris, Chlamydocarya, Citronella, Codiocarpus, Desmostachys, Discophora, Emmotum, Gastrolepis, Gonocaryum, Icacina, Iodes, Irvingbailey, Lasianthera, Leptaulus, Liriosma, Mappia, Medusanthera, Natsiatum, Pennantia, Phytocrene, Platea, Polyporandra, Poraqueiba, Pyrenacantha, Sarcostigma, Stemonurus, Trematosperma, Urandra.

(ii) FOR WOOD STRUCTURE

Alsodeiopsis, Anisomallon, Apodytes, Calatola, (Cantleya), (Cassinopsis), (Chlamydocarya), Citronella, (Dendrobangia), Desmostachys, Discophora, Emmotum, (Gastrolepis), Gonocaryum, (Grisollea), (Hosiea), (Humirianthera), (Icacina), (Lasianthera), (Lavigeria), Leptaulus, (Leretia), (Mappia), (Mappianthus), Medusanthera, (Merrilliodendron), (Miquelia), (Natsiatum), (Nothapodytes), (Oecopetalum), Ottoschulzia, Pennantia, (Phytocrene), (Pittosporopsis), Platea, (Pleurisanthes), (Polycephalum), (Polyporandra),

Poraqueiba, (Pyrenacantha), (Raphiostylis), (Rhyticaryum), (Sarcostigma), Stemonurus.

LITERATURE

(i) *On General Anatomy*

Bailey and Howard 81, Engler 629, 630, Francis 708, Heinzelman 2523, Howard 1091, 1092, 1093, 1094, 1095, 1096, 1097, 1098, Lendner 1357, Pfeiffer 1712, Scala 2018, Timmermans 2261.

(ii) *On Wood Structure*

Bailey and Howard 81, 82, 83, 84, Benoist 170, den Berger 182, Burgerstein 310, Chalk *et al.* 360, Cockrell 434, Cooper 461, Cozzo 494, Dadswell 525, Dadswell and Record 533, Desch 574, Francis 706, Howard 1088, Janssonius 1154, Kanehira 1206, Lecomte 1334, Metcalfe 1497, Normand 1619, Pfeiffer, H. 1712, Record 1843, 1851, 1853, Record and Hess 1886, Record and Mell 1894, Scott 2075, Tupper 2295, Williams 2426, 2430, 2431.

91. OCTOKNEMACEAE

(FIG. 86 on p. 372)

SUMMARY

This West African family has, until recently, been treated as comprising the trees and shrubs belonging to the single genus *Octoknema*. Some authorities now regard *Okoubaka aubrevillei* Pellegrin et D. Normand (syn. *Octoknema okoubaka* Aubr. et Pellegrin) as a distinct genus, a view which appears to be supported by differences in the structure of the wood. The anatomical features of the leaf and young stem of *Octoknema* which are given below are those recorded by Solereder and by Mildbraed (1534). The wood of the 2 genera exhibits the following structure. *Octoknema*. **Vessels** in numerous multiples, perforation plates scalariform, members very long. **Parenchyma** absent. **Rays** up to 3 cells wide, markedly heterogeneous. **Fibres** with simple pits, sometimes septate, moderately long. *Okoubaka*. **Vessels** solitary, perforations simple, members moderately to very short. **Parenchyma** apotracheal, diffuse. **Rays** up to 4 or 5 cells wide, homogeneous. **Fibres** with simple pits, but with bordered pits round the vessels, moderately long.

LEAF

Hairs tufted, e.g. in *Octoknema klainena* Pierre, and stellate, particularly in *O. affinis* Pierre. **Epidermis** composed of small, irregularly polyhedral cells. **Stomata** confined to the lower surface; ranunculaceous. Palisade tissue not clearly differentiated, but **mesophyll** more compact on the adaxial than on the abaxial side. Vascular bundles of the **veins** accompanied by strongly thickened fibres and **crystals** in the endodermis.

AXIS

YOUNG STEM

Cork arising in the sub-epidermis, the component cells thickened on the outer tangential and radial walls. Primary **cortex** containing stone cells with thickened, lignified walls, isolated or in small groups. Cortex also containing slightly thickened cells enclosing solitary crystals. **Pericycle** with a composite and continuous ring of sclerenchyma. **Phloem** including numerous

small bundles of fibres surrounded by crystalliferous cells. **Xylem** with evenly distributed vessels of equal size; walls with bordered pits; perforation plates frequently scalariform. Rays 1–2 cells wide; component cells often containing solitary crystals. **Pith** including groups of stone cells. **Crystals**, see 'Cortex', 'Phloem', and 'Rays'.

WOOD

Octoknema borealis Hutch. et J. M. Dalz. (Fig. 86 j and k)

Vessels moderately small (mean tang. diameter 50–100 μ); solitary and in numerous multiples of 2 or 3 cells; about 35 per sq. mm. Perforation plates scalariform, usually with fewer than 20 bars. Intervascular pitting opposite or intermediate between opposite and alternate, large; pits to ray cells commonly large, horizontally elongated and simple. Mean member length about 1.2–1.6 mm. **Parenchyma** absent. **Rays** up to 3 cells wide; commonly fused vertically to give rays 2 mm. or more high; uniseriate numerous, composed entirely of upright cells (apart from chambered crystalliferous cells); about 16 rays per mm.; markedly heterogeneous (Kribs's Type I), commonly with 10 or more marginal rows of square to upright cells. Chambered crystals numerous in the upright cells. **Fibres** with simple pits which have long apertures and trumpet-shaped canals and are almost entirely limited to the radial walls; sometimes septate. Walls moderately thin to thick. Mean length about 2.2 mm.

Okoubaka aubrevillei Pellegrin et D. Normand (*Octoknema okoubaka* Aubr. et Pellegr.)

Based on the description by D. Normand (1617). **Vessels** medium-sized (100–200 μ); exclusively solitary; about 4 per sq. mm. Perforations simple. Intervascular pitting alternate and small (?). Mean length about 0.25 mm. **Parenchyma** apotracheal, as numerous scattered cells and short uniseriate lines. Strands commonly of 2 cells. Tending to be storied. **Rays** up to 4–5 cells wide and about 1.5 mm. high; uniseriate rare or absent; about 4 rays per mm.; homogeneous (Kribs's Type II), composed of rather large procumbent cells. Crystals sometimes present in the ordinary cells. **Fibres** with simple pits. Walls very thick. Mean length about 2.0 mm. Fibre-tracheids occur about the vessels, with numerous bordered pits and thin walls.

TAXONOMIC NOTES

Although there has been much uncertainty concerning the taxonomic position of *Octoknema*, it is treated as a unigeneric family both by Mildbraed (1934) and Hutchinson (1913). The absence of any outstanding anatomical features makes it difficult to decide whether it has affinities with the Olacaceae. If it is related to this family the type of hair would suggest affinities with the Couleae.

Normand (1617) has drawn attention to the marked differences between the woods of *Octoknema* and *Okoubaka* and the separation of the genus *Okoubaka* appears to be well justified. Similar differences occur between genera recognized as belonging to the Olacaceae, and most of the features (with the exception of the homogeneous rays in *Okoubaka* and the absence of parenchyma from *Octoknema*) in the two genera which we are now considering

can be found in one or other of the genera which are generally accepted as members of the Olacaceae.

The wood structure of *Octoknema* is unspecialized, whereas that of *Okoubaka* is moderately highly specialized. Normand suggests that, while *Octoknema* has many wood characters in common with the Olacaceae, the structure of *Okoubaka* suggests affinity with the Santalaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Octoknema.

(ii) FOR WOOD STRUCTURE

Octoknema, (*Okoubaka*).

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113, Mildbraed 1534.

(ii) *On Wood Structure*

Cooper 461, Normand 1617, 1619, Record 1843, 1851.

92. OPILIACEAE

(FIG. 83 on p. 368; FIG. 84 on p. 368; FIG. 87 on p. 380; FIG. 89 on p. 388)

SUMMARY

A small family of trees, shrubs, or woody climbers from tropical regions, especially in Asia and Africa. Characteristic features include the occurrence of **cystoliths** in leaf and stem and branched, lignified cells in the **mesophyll**. The wood exhibits the following characters. **Vessels** exclusively solitary or with some multiples, perforations simple, intervacular pitting rare, alternate and small, pits to parenchyma similar, members moderately short. **Parenchyma** diffuse, strands usually of 2 cells. **Rays** up to 2-5 cells wide, with very few uniseriates, homogeneous; large cystoliths present in most of the genera. **Fibres** with simple or bordered pits, of medium length.

LEAF

Usually dorsiventral, but centric in *Opilia amentacea* Roxb. Multicellular **hairs**, branched like a stag's horn, recorded in certain species of *Cansjera* (Fig. 84 A). **Stomata** present on both surfaces in *Cansjera parvifolia* Kurz., rubiaceous in *Champereia* and *Opilia*. **Veins** connected by a branched system of spirally thickened, lignified cells, in *Agonandra*, *Cansjera*, *Lepionurus*, and *Opilia*. **Secretory elements**. Mucilage cells situated in the spongy mesophyll of *Agonandra* sp. and *Opilia* sp. Secretory cells with finely granular contents, readily stained with iodine, recorded in the lowest layer of the mesophyll of *Opilia amentacea*. **Crystals** absent. **Cystoliths**, arranged in groups of 2 to several in special cells, occur in the mesophyll of *Agonandra*, *Cansjera* (Fig. 83 A-B), *Lepionurus*, and *Opilia*.

AXIS

YOUNG STEM

Cork arising in the epidermis in certain species of *Champereia* and *Opilia*.

Pericycle with a composite and continuous ring of sclerenchyma in *Agonandra*, *Cansjera*, *Champereia*, *Lepionurus*, and *Opilia*. **Xylem** including vessels which are $33\ \mu$ in diameter in *Champereia*, exhibit spiral striation in *Opilia amentacea* Roxb., and have simple perforations in *Champereia* and *Opilia*. Rays 2–3 cells wide in *Champereia*; wood fibres provided with bordered pits and xylem parenchyma scanty in the same genus. **Cystoliths** (Fig. 87 A–D), similar to those in the leaf, generally present in the parenchyma of the axis, especially in the rays, of all of the genera.

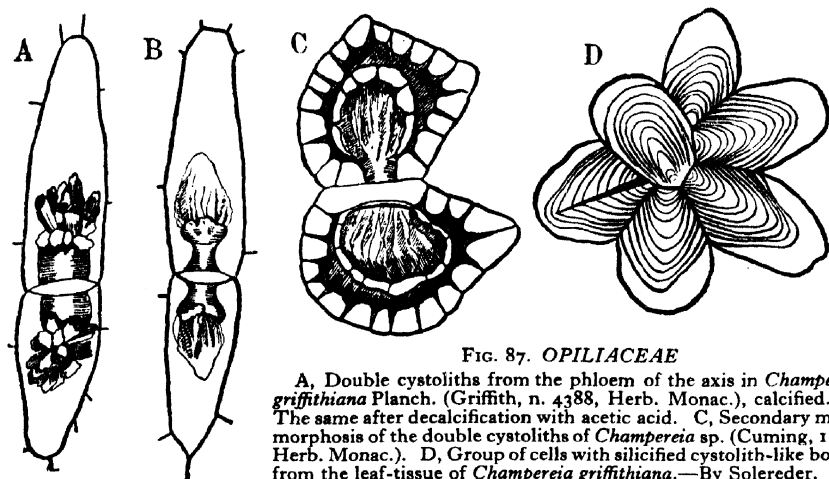


FIG. 87. OPILIACEAE

A, Double cystoliths from the phloem of the axis in *Champereia griffithiana* Planch. (Griffith, n. 4388, Herb. Monac.), calcified. B, The same after decalcification with acetic acid. C, Secondary metamorphosis of the double cystoliths of the *Champereia* sp. (Cuming, 1129, Herb. Monac.). D, Group of cells with silicified cystolith-like bodies from the leaf-tissue of *Champereia griffithiana*.—By Solereder.

WOOD (Fig. 89 A–C)

Vessels moderately small ($50\text{--}100\ \mu$ mean tangential diameter) to very small ($25\text{--}50\ \mu$); exclusively solitary in *Agonandra* and *Champereia*, with some multiples in *Opilia*; about 25 per sq. mm. Perforations simple. Intervascular pitting very rare, alternate and small; pits to ray and wood parenchyma small and round, sometimes striated. Mean member length $0.2\text{--}0.35\ \text{mm}$. (*Champereia*). **Parenchyma** apotracheal, as numerous scattered cells that sometimes tend to form short uniseriate lines. Strands usually of 2 cells, sometimes of 4 cells in *Champereia*, and with some fusiform cells in *Agonandra*. **Rays** up to 5 cells wide in *Champereia manillana* Merr., but seldom more than 2 cells wide in *Agonandra*; uniseriates very few, composed of procumbent cells; about 7 rays per mm.; homogeneous (Kribs's Type I). Large cells containing cystoliths of calcium carbonate (Fig. 89 B) observed or reported (1206, 1799, and 1818) in *Cansjera*, *Champereia*, *Lepionurus*, *Melientha*, *Opilia*, and *Rhopalopilina*, but absent from *Agonandra*. **Fibres**. Pits simple in *Champereia* but with small, moderately distinct borders in *Agonandra*, and distinctly bordered in *Opilia*. Walls thick. Mean length $1.0\text{--}1.4\ \text{mm}$.

TAXONOMIC NOTES

The genera *Agonandra*, *Cansjera*, *Lepionurus*, and *Opilia* constituted the tribe Opilieae of the Olacineae in the system of Bentham and Hooker. The Opiliaceae are treated as a distinct family by Sleumer (2130), and as a family

in the Olacales in Hutchinson's (1113) classification. The occurrence of a branched system of lignified cells in the leaf, and the development of cystoliths throughout all four of these genera are characters which indicate that they constitute a homogeneous group, and at the same time serve to differentiate them from the Olacaceae and Icacinaceae in which the same diagnostic characters have not been recorded. *Champereia* was included in the Santalaceae in the Bentham and Hooker system, but placed in the Opiliaceae in the classifications of both Engler and Hutchinson. On anatomical grounds it seems to belong to the Opiliaceae rather than the Santalaceae, the presence of the cystoliths which are such a characteristic feature of the Opiliaceae being especially interesting in this connexion. The family also appears to be unique in having cystoliths in the secondary xylem.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Agonandra, Cansjera, Champereia, Lepionurus, Opilia.

(ii) FOR WOOD STRUCTURE

Agonandra, (Cansjera), Champereia, (Lepionurus), (Melientha), Opilia, (Rhopalopilia).

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113, Sleumer 2130.

(ii) *On Wood Structure*

Kanehira 1206, 1209, Record 1799, 1818, 1851, 1853.

93. AQUIFOLIACEAE

(FIG. 88 on p. 382; FIG. 89 on p. 388)

SUMMARY

(i) GENERAL

A widely distributed family of trees and shrubs, most species being evergreen. Practically all of the anatomical observations which have been made refer to the single genus *Ilex*. The description which follows may be taken to refer to this genus only, except where stated to the contrary. The family is anatomically homogeneous, except in so far as there are minor differences, especially in leaf structure, between the deciduous and evergreen species. The **epidermis** of the leaf is frequently many-layered and the component cells mucilaginous. **Hypoderm** has also been recorded on the upper side of the leaf of certain species, but it seems probable that true hypoderm has not always been clearly distinguished from an epidermis of more than one layer. **Cork warts** on the lower surface of the leaf are characteristic of some species, and the **leaf margin** is frequently strengthened mechanically by cuticularized or sclerenchymatous tissues. The **hairs** are usually infrequent but, where present, generally consist of small unicellular trichomes, although multicellular, thin-walled trichomes have been recorded in certain deciduous species. **Stomata** ranunculaceous; confined to the lower surface. In the

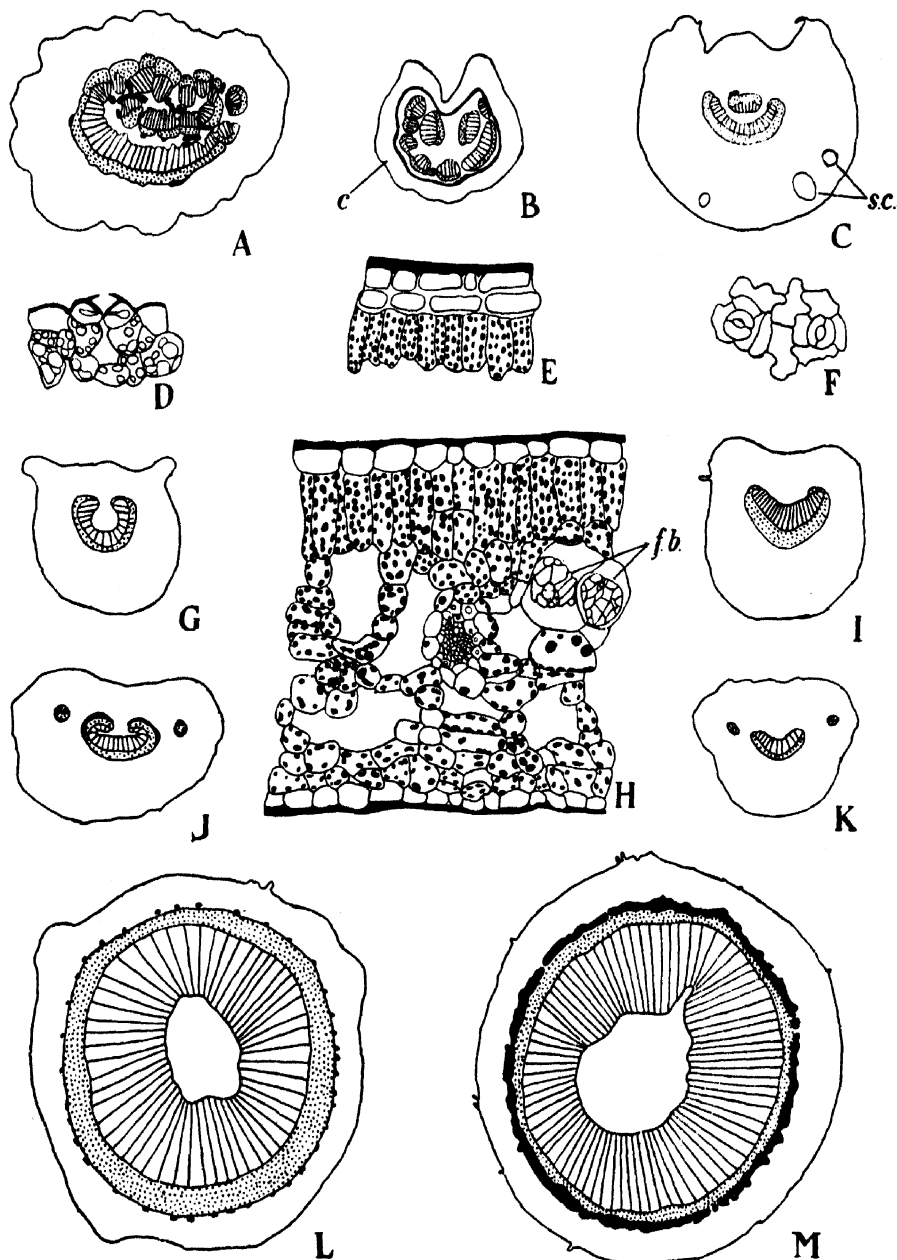


FIG. 88. *GOUPIACEAE*, A; *CELASTRACEAE*, B, D, and G; *HIPPOCRATEACEAE*, C; *AQUIFOLIACEAE*, E-F, H, and J-K; *ICACINACEAE*, I and L-M

A, *Goupia glabra* Aubl. Petiole $\times 22$. B, *Kurrimia pulcherrima* Wall. Petiole $\times 15$. C, *Salacia roxburghii* Wall. Petiole $\times 15$. D, *Euonymus radicans* Sieb. Stomata on lower surface $\times 250$. E, *Ilex aquifolium* Linn. T.S. lamina; adaxial part. $\times 167$. F, *I. paraguariensis* St. Hil. Stomata on upper surface $\times 167$. G, *Catha edulis* Forsk. Petiole $\times 15$. H, *Ilex paraguariensis* St. Hil. T.S. lamina $\times 167$. I, *Apodytes dimidiata* E. Mey. Petiole $\times 15$. J, *Ilex paraguariensis* St. Hil. Petiole $\times 15$. K, *I. aquifolium* Linn. Petiole $\times 15$. L, *Apodytes dimidiata* E. Mey. Stem $\times 15$. M, *Miquelia* sp. Stem $\times 15$. c. Cortex with abundant tanniniferous cells. f.b. Fat bodies. s.c. Secretory cavities.

xylem of the young stem the wood fibres are provided with bordered pits, and the vessels with scalariform perforation plates.

(ii) WOOD

Vessels small, often in marked radial groups or lines, spiral thickening usually present in *Ilex* and *Byronia*, perforation plates exclusively scalariform and mostly with many bars, intervacular pitting usually opposite; members moderately to very long. **Parenchyma** moderately abundant, diffuse. **Rays** of 2 distinct sizes, the larger 5–15 cells wide and 2–5 mm. high, heterogeneous. **Fibres** with distinctly bordered pits; spirally thickened in *Ilex*; of medium length to moderately long.

LEAF

Dorsiventral. **Cuticle** very thin in *Nemopanthus* and in certain species of *Ilex*, e.g. *I. laevigata* (Pursh.) Gray and *I. verticillata* (L.) Gray, but very thick in most species of *Ilex* and consisting of 2 distinct layers in some. **Hairs** rare, but where present usually consisting of unicellular trichomes with the lumina almost or completely obliterated. Long, multicellular, thin-walled trichomes recorded in *I. laevigata* and *I. verticillata*. **Cork warts**, resembling lenticels and consisting of hemispherical groups of cells with suberized walls radiating from the centre of the hemisphere, abundant on the lower surface of certain species of *Ilex*. **Margins** of the leaf strengthened mechanically in various ways in different species: (i) by cuticular thickenings; (ii) by sclerenchymatous tissue containing chlorophyll (*I. insignis* Hook. f.); (iii) by a sheath of sclerenchyma (*I. aquifolium* Linn.). **Epidermis** consisting of 1–3 layers of cells in different species of *Ilex*; the component cells partly or wholly mucilaginous in a considerable number of species, sometimes penetrating deeply into the mesophyll. Lower epidermis with considerable thickening and pitting of the inner walls in *I. affinis* Gardn. **Hypoderm**, not to be confused with a many-layered epidermis, occurs in certain species, notably *I. aquifolium* (Fig. 88 E). **Stomata** (Fig. 88 F) confined to the lower surface; sometimes surrounded by a rampart of cuticle; ranunculaceous. (Solleder's statement that some semblance of subsidiary cells occurs in *I. paraguariensis* St. Hil. has not been confirmed by observation.) **Mesophyll** including 2 or more layers of palisade tissue in species with coriaceous leaves, but only 1-layered in deciduous species such as *I. laevigata* and *I. verticillata*. Spongy mesophyll somewhat variable in different species; intercellular spaces few in *I. decidua* Walt. but well developed in *I. insignis* Hook. f. and *I. latifolia* Thunb. Vascular bundles of the **veins** accompanied by a varying amount of sclerenchyma in different species of *Ilex*. Phloem of the midrib stated to form a continuous band round the xylem in the evergreen species *I. opaca* Ait. and *I. glabra* (L.) Gray, but according to Holm (1953) the bundle is crescent-shaped in *I. laevigata* and *I. verticillata*. Midrib very prominent on the upper side in *I. glabra*, but most prominent on the lower side in a majority of the species. **Petiole**, in transverse sections, exhibiting an arc-shaped vascular strand, relatively open in some species, e.g. *Ilex aquifolium* (Fig. 85 K), but with strongly incurved ends in others, e.g. in *Ilex paraguariensis* (Fig. 85 J); often accompanied by 2 very small accessory strands. Vascular strand accompanied externally by sclerenchyma varying in amount in different species, and

almost completely absent from *I. glabra*. **Fat bodies** common in the mesophyll. **Crystals** exclusively clustered, sometimes occurring in roundish idioblasts. Epidermis stated to contain sphaerocrystalline masses, possibly consisting of **hesperidin**, in varieties of *I. paltorioides* Reiss. and a few other species.

AXIS

YOUNG STEM

Cuticle very thick, smooth in some species (e.g. *I. aquifolium* Linn.), but granular in others (e.g. *I. glabra* (L.) Gray). **Cork** arising in the epidermis or hypodermis; cork cells with unusually thick walls. **Epidermis** tending to persist even after the formation of cork. Primary **cortex** parenchymatous when young, but outer part tending to become slightly collenchymatous in *I. aquifolium* and other species. Stone cells have been recorded in the cortex, but none were observed in any of the species of *Ilex* available for examination. **Pericycle** containing isolated strands of fibres in young stems, but becoming united by stone cells to form a composite and continuous ring in species of *Byronia* and *Ilex*. **Xylem** and **phloem** commonly traversed by broad rays. Vessels with scalariform perforation plates. Solitary and clustered **crystals** occur in the cortex.

WOOD (Fig. 89 D-E)

Vessels mostly very small (less than 50 μ mean tangential diameter) and sometimes extremely small, but rather larger in some species of *Ilex*, particularly in *I. cymosa* Bl. (75 μ); radial multiples of 4 or more common in *Ilex* (except *I. cymosa* Bl.) and *Byronia* and often imparting a marked radial pattern to these woods, sometimes in clusters, and with a tendency to local tangential arrangement in some species of *Ilex*; difficult to count satisfactorily owing to the groups, fewest (about 7 per mm.) in *I. cymosa* Bl.; Kanehira (1206) gives the upper limit for *Ilex* as 120 per mm.; more numerous at the beginning of the ring in some species of *Ilex* and ring-porous in *Nemopanthus* (533), typically with well-marked spiral thickening in temperate species of *Ilex* and *Byronia*, but Record (1894) lists 3 species of *Ilex* without spiral thickening, to which may be added *I. cymosa* Bl. Perforation plates exclusively scalariform, with more than 20 bars except in *Nemopanthus*. Intervascular pitting opposite, sometimes scalariform in *Ilex* (Record, 1818, 1853) and sometimes nearly alternate in *I. aquifolium* L.; pits to ray and parenchyma cells similar to the intervascular pitting, but sometimes elongated or unilaterally compound in *Ilex*. Deposits and tyloses not observed but calcium oxalate recorded in callus tissue of *I. opaca* Ait. (Record, 1818). Mean member length 0.9–1.3 mm. **Parenchyma** moderately abundant, apotracheal, diffuse, as scattered cells or short uniseriate lines of a few cells. Chambered cells containing crystals moderately common in *I. cymosa* Bl. Strands commonly of 8 cells. **Rays** of 2 distinct sizes, uniseriate or wide and multiseriate, the larger rays mostly between 4 and 10 cells wide, more than 10 cells wide in a few species of *Ilex*, e.g. *I. cymosa* Bl., *I. hanceana* Max., and *I. mitis* (L.) Radlk., and in *Phelline*; maximum height 2–5 mm.; uniseriate rays, composed of high upright cells, usually abundant; Loesener, according to Solereder, states that the rays are exclusively uniseriate in *I. verticillata*; about 7–15 rays

per mm.; heterogeneous (Kribs's Type I), the larger rays with between 4 and 10 marginal rows of upright cells in most species, usually with fewer than 4 rows in *I. hanceana* Max., *I. mitis* (L.) Radlk., and *Phelline* and with more than 10 rows in *I. aquifolium* L. and *Byronia*; with sheath cells, except in *Nemopanthus*; crystals in chambered cells observed in *I. cymosa* Bl. and recorded by Kanehira (1206) for several Formosan species of *Ilex*. **Fibres** with distinctly bordered pits (borders rather small in *I. cymosa* Bl.), more numerous on the radial than on the tangential walls; with moderately thin to moderately thick walls; spiral thickening characteristic of temperate species of *Ilex*; absent from *I. cymosa* Bl. and 3 species listed by Record (1894). Mean length 1.3–2.1 mm. **Growth ring** formation in *Ilex* has been described by Coster (481).

ROOT

The root structure of *Ilex* has been described by Weber (2380).

ECONOMIC USES

Maté, Yerba Maté, or Paraguay Tea is the product of various cultivated forms and varieties of *Ilex paraguariensis* St. Hil. Other species of *Ilex*, as well as unrelated plants such as species of *Citronella*, *Rapanea*, *Rudgea* (see 'Rubiaceae'), and *Symplocos*, have been used as substitutes according to Lendner (1357) and Scala (2024). Yaupon or Yapon tea is the product of *Ilex cassine* Walt.

The leaf of *Ilex paraguariensis* (Fig. 85 H and J) exhibits the following structure. Cells of the upper epidermis with thick, straight anticlinal walls. Cuticle thick and often striated, but the amount of striation somewhat variable. Stomata confined to the lower surface, surrounded by about 3–5 ordinary epidermal cells with sinuous anticlinal walls. Palisade tissue very variable in different samples, usually consisting of about 3 layers of cells, but the individual cells almost isodiametric in some samples and very elongated in others. Fat bodies sometimes present in this tissue. Spongy mesophyll with abundant intercellular spaces. Large cluster crystals fairly common in the mesophyll as well as in the parenchyma of the midrib. Midrib with a single vascular strand, consisting of a cylinder of xylem enclosing a lignified pith; xylem almost or completely surrounded by phloem, the whole conducting system being enclosed in a ring of sclerenchyma. The main vascular strand of the petiole is similar to that of the midrib, but the xylem has the form of an arc with very much incurved margins in some specimens. Small accessory strands also occur in the petiole.

The European and American Hollies (*Ilex aquifolium* L. and *I. opaca* Ait.) furnish white woods that are widely used for marquetry and inlay work and are sometimes dyed to imitate ebony.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Byronia, *Ilex*,* *Nemopanthus*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(*Byronia*), *Ilex*, (*Nemopanthus*), (*Phelline*).

LITERATURE

(i) *On General Anatomy*

Holm 1053, Lendner 1357, Rivett 1943, Scala 2024, Weber 2380.

(ii) *On Wood Structure*

den Berger 179, 182, Brown, F. B. H. 280, Brown, H. P. 288, 289, Chalk and Rendle 365, Coster 481, Cozzo 494, Dadswell and Record 533, Desch 574, Descole 576, Giordano 786, Greguss 2522, Howard 1088, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Record 1783, 1800, 1803, 1818, 1843, 1851, 1853, Record and Hess 1886, Record and Mell 1894, Tang 2231, Tupper 2295, Williams 2430, Yamabayashi 2478.

94. CYRILLACEAE

(FIG. 89 on p. 388)

SUMMARY

A small family of shrubs from the U.S.A., Brazil, and intervening regions. Its anatomy has been investigated by Solereder and Beauvisage (163). The wood exhibits the following characters. **Vessels** very small and very numerous; perforation plates exclusively scalariform with numerous fine, closely spaced bars; intervacular pitting scalariform to opposite, pits to ray cells and parenchyma similar to the opposite intervacular pits. Members of medium length to moderately long. **Parenchyma** diffuse, or diffuse and scanty paratracheal. **Rays** mostly 4–5 cells wide, with few uniseriate rays and these commonly only 1 or 2 cells high; heterogeneous. **Fibres** with numerous distinctly bordered pits; of medium length.

LEAF

High, irregularly arranged ridges of **cuticle** on the lower side in *Cliftonia nitida* Gaertn. f. Cells of the **epidermis** with straight anticlinal, sometimes mucilaginous walls. **Stomata** in *Cliftonia nitida* and *Cyrilla racemiflora* Linn. confined to the lower surface; surrounded by fairly numerous ordinary epidermal cells. **Mesophyll** consisting wholly of palisade tissue in *Cliftonia nitida* and *Cyrilla racemiflora* according to Solereder, but 2 layers of palisade tissue present in *Cyrilla* according to Beauvisage (163). Vascular bundles of the **veins** accompanied by sclerenchyma. **Petiole** of *Cyrilla* stated by Beauvisage (163) to be complex in structure; exhibiting, in transverse sections, a vascular strand having the form of a complete ring, depressed on the adaxial side and accompanied by an accessory collateral strand, the whole vascular system being surrounded by a continuous sheath of sclerenchyma. Both solitary and clustered **crystals** occur; especially large clustered ones recorded by Beauvisage (163) in *Cyrilla*.

AXIS

YOUNG STEM

Cork very precocious in development, arising in the innermost part of the primary cortex; accompanied by phelloderm. Primary **cortex** containing numerous sclerosed parenchymatous cells with wide lumina; but soon becoming detached owing to the early formation of the deep-seated cork. **Pericycle** devoid of fibres. Parenchyma in the outer part of the **phloem** becoming sclerosed after cork has been formed according to Solereder, but

isolated and infrequent fibres stated by Beauvisage (163) to occur in the phloem. **Xylem** including numerous fairly uniformly distributed vessels, having scalariform perforation plates with 20–30 bars. Wood fibres with bordered pits. **Pith** sclerosed.

WOOD (Fig. 89 F–G)

Vessels very small ($25\text{--}50\ \mu$ mean tangential diameter), mostly solitary, except for the apparent tangential pairs produced by overlapping ends, but with a tendency to true tangential groups in the late wood of *Cliftonia*; extremely numerous, especially in *Cliftonia* (about 140 per mm.). Occasionally with a tendency to be semi-ring-porous (Heimsch 938). Perforation plates exclusively scalariform, with up to 30–50 fine, closely spaced bars. Intervascular pitting scalariform to opposite, small; pits to ray parenchyma cells similar to the opposite intervacular pits; pits to ray cells usually limited to the upright cells; walls unusually thin. Mean member length about 0.8 mm. (100). **Parenchyma** moderately abundant in *Cyrilla* (Fig. 89 F), diffuse, as isolated cells scattered among the fibres; less abundant in *Cliftonia* and mostly as occasional cells touching the vessels. Sometimes containing dark deposits. Strands of 4–8 cells. **Rays** usually up to 4, occasionally 5 or 6 cells wide, and up to 8 cells wide in a few species (1886); less than 1 mm. high; uniseriate few, often only 1 or 2 cells high and composed almost entirely of square to upright cells; about 6 rays per mm.; heterogeneous (Kribs's Type II A, sometimes almost II B), usually with only a single marginal row of distinctly upright cells; dark deposits common. Heimsch (938) notes crystals in a single species. **Fibres** with numerous distinctly bordered pits on both radial and tangential walls, with thin to thick walls in different parts of the growth ring; mean length about 1.0 mm. (100).

TAXONOMIC NOTES

The wood structure is of an unspecialized type.

GENERA DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Cliftonia and *Cyrilla*.

LITERATURE

(i) *On General Anatomy*
Beauvisage 163.

(ii) *On Wood Structure*

Heimsch 938, Howard 1088, Record 1783, 1843, 1851, 1853, Record and Hess 1886.

95. CELASTRACEAE

(FIG. 88 on p. 382; FIG. 90 on p. 392)

SUMMARY

(i) GENERAL

A widely distributed family consisting mostly of small trees or shrubs but a few species are climbers. Outstanding anatomical characters for the whole family appear to be lacking. Whilst the **xylem** in young stems of most of

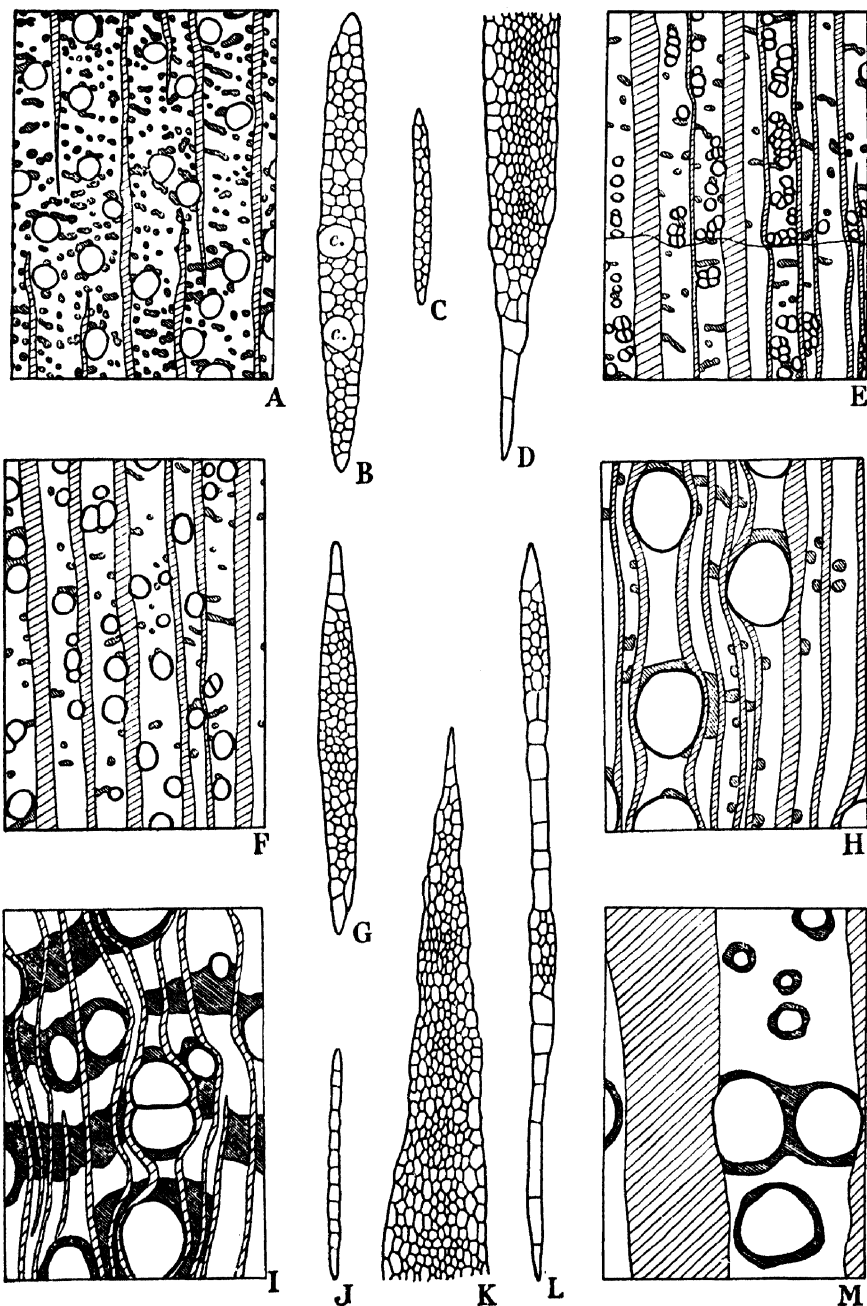


FIG. 89. OPILIIACEAE, A-C; AQUIFOLIACEAE, D-E; CYRILLACEAE, F-G. GOUPIACEAE, H and L; HIPPOCRATEACEAE, I-J and M.

A, *Agonandra brasiliensis* Benth. et Hook. B, *Champereia manillana* Merrill. C, *Agonandra brasiliensis* Benth. et Hook. D, *Ilex mitis* Radlk. E, *I. aquifolium* Linn. F, *Cyrilla racemiflora* Linn. G, *Cliftonia ligustrina* Spreng. H, *Goupia glabra* Aubl. I, *Salacia megistophylla* Standley. J, *S. reticulata* Wight. K, *Hippocratea malpighiaefolia* Rudge. L, *Goupia glabra* Aubl. M, *Hippocratea malpighiaefolia* Rudge.

c. Cell containing cystolith.

the species which have been investigated is characterized by small vessels which are frequently solitary and possess simple perforations, the genera *Kurrimia* and *Perrottetia* are distinguishable from the other Celastraceae examined in possessing scalariform perforation plates in the vessels. According to Solereder scalariform perforation plates also occur in *Elaeodendron* and *Glossopetalon*, but their presence was not confirmed in *Elaeodendron glaucum* Pers. by direct observation. Characteristic **secretory sacs** or **canals** filled with granular material, which is stated to resemble rubber, occur in the phloem of the axis as well as in the vascular bundles of the leaf veins in certain genera. **Hairs** are infrequent, but when present are unicellular or uniseriate, the former sometimes more like papillae. The **epidermis** of the leaf sometimes consists of several layers, or **hypoderm** may be present. The **mesophyll** contains sclerenchymatous idioblasts in certain genera, whilst fat bodies occur in some of the cells in the same tissue.

(ii) Wood

Vessels typically small, numerous and solitary, though multiples of 2-3 cells are characteristic of some species; with flame-like arrangement in *Otherodendron*; sometimes ring-porous or semi-ring-porous, and occasionally with spiral thickening; perforation plates usually simple but scalariform in a few species; intervacular pitting and pits to ray and parenchyma alternate, very small in most genera. Members of medium length to moderately long. **Parenchyma** very variable in type and amount; commonly very sparse or absent, diffuse or in broad multiseriate bands in some genera, vasicentric or transitional between banded and aliform in a few others. **Rays** in some genera exclusively uniseriate, homogeneous, and with conspicuous intercellular spaces; in other genera, 2-8 (mostly 3-4) cells wide and markedly heterogeneous. **Fibres**. The ground tissue typically composed of fibre-tracheids with numerous, distinctly bordered pits, but occasionally of septate fibres with simple pits; septate fibres often occur in multiseriate bands, comparable in distribution to parenchyma bands; very occasionally with spiral thickening; of medium length to moderately long.

LEAF

Generally dorsiventral, but isobilateral in certain species, for example, of *Gymnosporia*, *Maytenus*, and *Mortonia*. **Hairs** infrequent; short unicellular trichomes recorded in species of *Euonymus*, *Fraunhoferia*, *Mystroxydon*; papillose hairs of 1 or 2 cells in *Tripterygium*; papilla-like trichomes accompanied by long hairs with thin transverse walls in *Fraunhoferia* and *Wimmeria*; unicellular hairs, sometimes 2-armed, in *Myginda*. **Cuticle** striated in certain species of *Microtropis*, *Polycardia*, and *Zinowiewia*. (It is not quite clear what is meant when Solereder describes the cuticle as being pitted in species of *Catha* and *Polycardia*. Examination of a few species indicates that the cuticle is capable of becoming separated into 2 layers, also that there are small areas rather suggestive of pits, in which the cuticle is thinner. Whether these thin places in the cuticle represent the pits mentioned by Solereder is uncertain.) **Epidermis** palisade-like in certain species of *Cassine*, *Gymnosporia*, *Kokoona*, *Maurocenia*, *Mortonia*, *Polycardia*, *Pterocelastrus*, and *Putterlickia*; consisting

wholly or locally of 2-3 layers in species of *Catha*, *Elaeodendron*, *Gymnosporia*, and *Plenckia*. Cells of the upper epidermis occupy nearly half the width of the lamina in *Tripterygium forrestii* Loes. **Hypoderm** frequently present, either on the upper side alone or towards both surfaces, in species of *Cassine*, *Celastrus*, *Denhamia*, *Elaeodendron*, *Euonymus*, *Gyminda*, *Gymnosporia*, *Maurocenia*, *Maytenus*, *Myginda*, *Mystroxydon*, *Rhacoma*, and *Schaefferia*. In the literature true hypoderm has probably not always been clearly distinguished from an epidermis of more than 1 layer. Epidermis containing scanty or plentiful crystal cells (crystal idioblasts) in species of *Catha*, *Denhamia*, *Elaeodendron*, *Euonymus*, *Gyminda*, *Kurrimia*, *Lophopetalum*, *Maytenus*, *Microtropis*, *Myginda*, *Pleurostylia*, *Siphonodon*, *Wimmeria* (see also 'Crystals' below). **Stomata** (Fig. 88 D) usually confined to the lower surface, but present on the upper side as well in species of *Gymnosporia*, *Maytenus*, and *Mortonia*; usually cruciferous to ranunculaceous but rubiaceous in *Kurrimia*; guard cells surrounded by a rosette of smaller epidermal cells in *Mortonia*. Guard cells stated by Rehfoos (1904) to become divided, the daughter cells being situated below them, in species of *Catha*, *Celastrus*, and *Euonymus*. **Mesophyll**. Palisade cells transversely divided in species of *Mortonia* and *Pachystima*; homogeneous in species of *Gymnosporia*, *Myginda*, and *Zinowiewia*. Sclerenchymatous idioblasts present in the mesophyll of species of *Maurocenia*, *Maytenus*, *Microtropis*, *Pterocelastrus*, and *Schaefferia*. Vascular bundles of the **veins** generally accompanied by sclerenchyma; smaller veins vertically transcurrent in species of *Cassine*, *Plenckia*, *Tripterygium*, and *Wimmeria*. Terminal tracheids enlarged in *Myginda* and *Schaefferia*. **Midrib** with a simple vascular strand in species of *Catha* and *Euonymus*; with 2 central bundles in *Glyptopetalum* and *Microtropis*. Vascular strand, in transverse sections through the distal end of the **petiole**, appearing arc-shaped in most of the plants investigated, which include species of *Catha* (Fig. 88 G), *Celastrus* (ends of the strand very much incurved in some species), *Euonymus* (nearly closed in some species), *Glyptopetalum*, *Microtropis*, *Perrottetia*, *Tripterygium*; vascular strand closed in members of certain other genera including *Cassine*, *Elaeodendron*, *Lophopetalum*, and *Maytenus*. Petiole of *Kurrimia pulcherrima* Wall. (Fig. 88 B) with an almost closed but interrupted cylinder of xylem and phloem surrounding 2 well-defined medullary bundles. Medullary bundles in the petiole also recorded by Loesner (1389) in *Lophopetalum*. Accessory bundles present outside the main petiolar strand in species of *Celastrus*, *Euonymus*, *Perrottetia*, and *Tripterygium*. Pericyclic region of the petiole containing abundant sclerenchyma in species of *Cassine*, *Catha*, *Celastrus*, *Kurrimia*, *Maytenus*; sclerenchyma not well developed in, or almost absent from, species of *Celastrus*, *Elaeodendron*, *Euonymus*, *Glyptopetalum*, *Microtropis*, *Perrottetia*, and *Tripterygium*. 'Cortex' of petiole containing irregularly shaped sclerotic cells in *Maytenus* sp. Long **secretory sacs** with rubber-like contents (see also 'Axis') recorded in the pericycle of the veins in certain species of *Celastrus*; similar sacs also recorded in the position normally occupied by phloem fibres, and sometimes in the mesophyll as well in numerous species of *Wimmeria*. **Secretory canals** with yellow contents stated to accompany the veins and also to be situated at the leaf margins of *Mortonia greggii* Gray; similar canals but devoid of contents recorded in the leaf margins of certain species of *Pachystima*. **Tanniniferous cells** recorded in

the mesophyll of species of *Cassine*, *Euonymus*, *Gymnosporia*, *Maytenus*, *Microtropis*, *Myginda*, *Pachystima*, *Siphonodon*, *Wimmeria*, and *Zinowiewia*. Similar cells observed in the 'cortex' of the petiole of species of *Cassine*, *Catha*, and *Elaeodendron*. **Crystals** solitary or clustered, sometimes accompanied by crystal-sand; cluster crystals often abundant in the cortical region of the petiole. Solereder's more complete statements concerning their occurrence and distribution need reinvestigation. Crystals stated to occur in continuous layers of special cells in certain species of *Pleurostyliia* and *Pterocelastrus*; sometimes present in septate palisade cells in *Elaeodendron* and *Mortonia* or in crystal idioblasts in the mesophyll of *Cassine*, *Catha*, *Celastrus*, and *Euonymus*. See also 'Epidermis' and 'Hypoderm'.

AXIS

YOUNG STEM

Cork usually arising in the sub-epidermis, but originating in the epidermis itself in *Euonymus* and *Microtropis*; formed in the outer part of the primary cortex in *Elaeodendron* and *Lauridia*, and in the inner part of the cortex in *Myginda* and *Tripterygium*. Cork cells often tabular and thin-walled, but thickened tangential walls occur in species of *Celastrus*, *Elaeodendron*, *Kurrimia*, *Maytenus*, *Microtropis*, and *Tripterygium* (very thick-walled, pitted cells). **Corky outgrowths**, resembling but apparently distinct from lenticels, stated to arise from the cortical parenchyma of *Euonymus verrucosa* Scop. **Cortex** frequently containing tanniniferous cells, notably in species of *Cassine*, *Catha*, *Celastrus*, *Elaeodendron*, *Gymnosporia*, *Microtropis*. Stone cells present in the cortex of species of *Cassine*, *Elaeodendron*, *Maytenus*, *Microtropis*, and bundles of fibres in the same region in *Euonymus*. Outer layers of the cortex consisting of palisade cells in *Euonymus americana* Linn. but not in *E. atropurpurea* Jacq. **Pericycle** often containing strands of fibres, notably in species of *Catha*, *Elaeodendron*, *Euonymus*, and *Perrottetia*; with a composite and continuous ring of sclerenchyma in species of *Cassine*, *Celastrus*, *Fraunhoferia*, *Glyptopetalum*, *Kurrimia*, *Lophopetalum*, *Maurocenia*, *Maytenus*, *Microtropis*, and *Tripterygium*; pericyclic fibres apparently absent from certain species of *Celastrus* and *Euonymus*, but stated to occur in the form of a continuous ring in other members of the last genus. **Phloem** and **xylem** usually constituting closed cylinders traversed by narrow rays, but stated by Colas (446) to be in the form of bundles separated by conspicuous medullary rays in *Maytenus* sp. Phloem containing large stone cells in old material of *Euonymus europaeus* Linn. and in *Kurrimia pulcherrima* Wall. Fibres stated by Beauvisage (163) to occur in the phloem of species of *Catha*. Xylem including vessels which are commonly of uniform, small diameter, notably in species of *Cassine*, *Catha* (radial diameter seldom exceeding $33\ \mu$ in first-year stems of *Catha edulis* Forsk.), *Celastrus*, *Elaeodendron*, *Euonymus* (radial diameter seldom exceeding $50\ \mu$ in first-year stems of *Euonymus europaeus*), *Maytenus*; mostly solitary or in pairs and up to about $85\ \mu$ in radial diameter in *Tripterygium forrestii* Loes.; in radial rows of *Kurrimia pulcherrima* Wall. and tending to be similar in *Microtropis discolor* Wall. Vessels of the first year's wood in certain species of *Celastrus* are very small and infrequent compared with those developed during subsequent seasons. Perforations believed to be exclusively simple in

species of *Cassine*, *Celastrus*, *Elaeodendron*, *Euonymus*, *Microtropis*, and *Tripterygium*, but scalariform perforation plates observed in *Kurrimia* and *Perrottetia*. Pith generally homogeneous, but frequently heterogeneous in

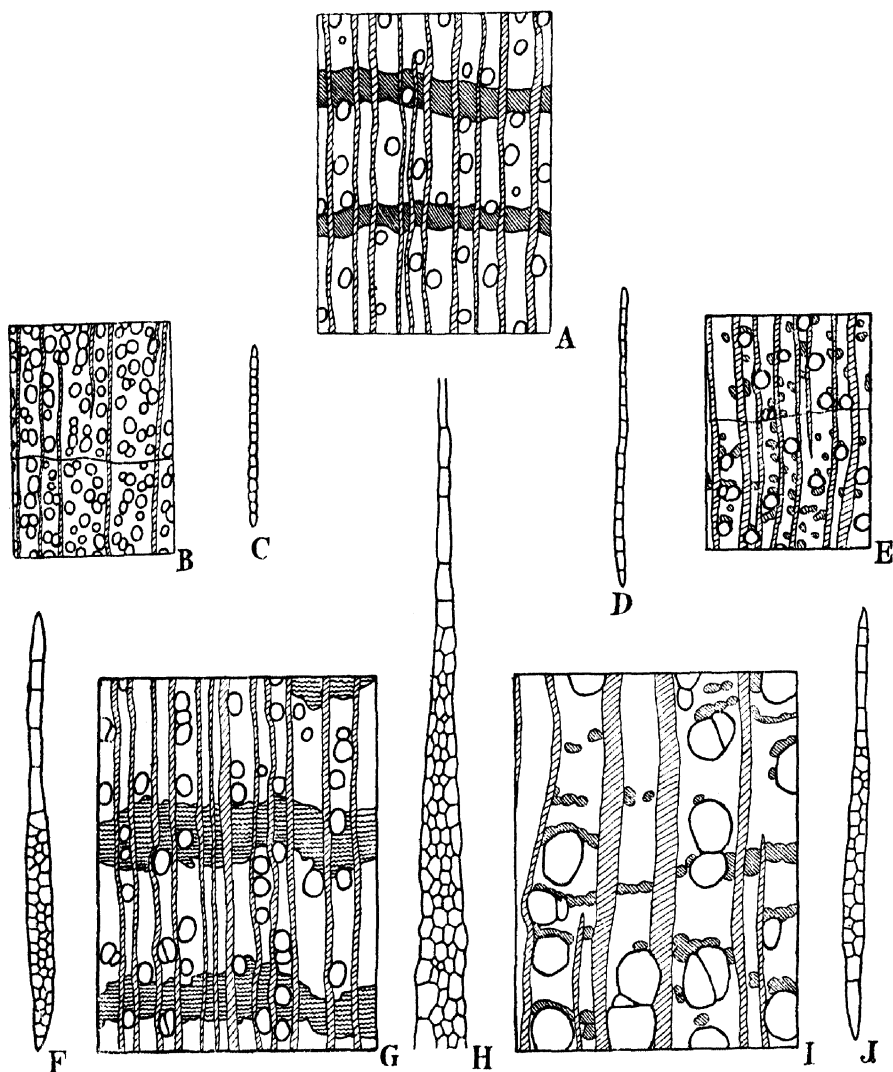


FIG. 90. CELASTRACEAE

A, *Celastrus peduncularis* Sind. B, *Euonymus europaeus* Linn. C, *E. europaeus* Linn. D, *Lophopetalum fimbriatum* Wight. E, *Myginda eucymosa* Loss et Pitt. F, *Elaeodendron capense* Eckl. et Zeyh. G, *E. capense* Eckl. et Zeyh. H, *Kurrimia paniculata* Wall. I, *K. paniculata* Wall. J, *Pterocelastrus tricuspidatus* Walp.

Gymnosporia, *Lophopetalum*, *Microtropis*, *Perrottetia*, *Polycardia*, and *Pterocelastrus*; sometimes containing stone cells in *Kokoona* and *Maytenus*; tanniniferous cells in species of *Cassine*, *Catha*, *Celastrus*, *Elaeodendron*, *Microtropis*, and *Tripterygium*. Elongated **secretory cells** sometimes occur in the phloem

of species of *Catha*, *Celastrus*, *Elaeodendron* (very elongated, comparable with canals), and *Microtropis*. See also 'Cortex' above. Secretory cells observed in the phloem of *Celastrus rugosus* Rehd. et Wil. and *Euonymus europaeus* Linn. The secretory cells were examined particularly in *Euonymus europaeus*, where they are apparently absent from the very young stem but occur in the secondary phloem of older material, especially when this tissue clearly constitutes part of the bark. They appear to have rare transverse septa and to be filled with granular material, stained yellow by chlor-zinc-iodide.

WOOD (Fig. 90)

Vessels typically very small (less than $50\ \mu$ mean tangential diameter), extremely small in some genera, e.g. *Gymnosporia*, *Maurocenia*, and *Plenckia*, moderately small ($100\text{--}200\ \mu$) in *Caryospermum*, *Kurrimia*, *Lophopetalum*, and *Perrottetia*; exclusively solitary, or nearly so, in *Cassine*, *Celastrus*, *Elaeodendron*, *Lophopetalum littoralis* Ridl. and *L. maingayi* Ridl., *Maurocenia*, *Mortonia*, *Myginda*, *Plenckia*, *Pleurostyli*, *Perrottetia*, *Pterocelastrus*, and *Schaefferia*, radial flames reported in *Othierodendron* (Kanehira 1209), radial multiples of 2 or 3 cells common in the remainder, sometimes up to 4 cells in some species of *Lophopetalum* and *Maytenus*; typically numerous; fewer than 5 per sq. mm. in *Perrottetia*, 5–20 per sq. mm. in *Kookoona*, *Kurrimia*, *Lophopetalum*, and *Siphonodon*, 20–40 per sq. mm. in *Caryospermum*, *Cassine*, *Maytenus* p.p., *Myginda*, and *Pterocelastrus*, 40 to over 200 in the remaining genera; ring-porous or semi-ring-porous in *Celastrus* (Record 1853), *Gymnosporia buxifolia* (L.) Szysz., *Maurocenia*, *Mortonia*, *Pachystima* (Record 1853), *Plenckia*, and *Rhacoma*; spiral thickening sometimes present in *Austroplenckia* (1886), *Celastrus*, *Euonymus*, *Maytenus* p.p., *Mortonia* (1886), *Pachystima* (1886), and *Plenckia*; Solereder records spiral thickening also in *Tripterygium* and Record (1851) in *Lophopetalum*, though the latter could not be confirmed in the material examined. Perforation plates scalariform in *Cassine* p.p., *Elaeodendron*, *Kurrimia*, and *Perrottetia*¹ with fewer than 10 bars, except in *Perrottetia* (1209). Solereder quotes Loesner as describing the perforations of *Cassine* as exclusively simple, which though applicable to *C. capensis* Linn., is not true of *C. crocea* (Thunb.) O. Kze. in which the perforation plates are exclusively scalariform. Intervascular pitting alternate, typically very small except in *Caryospermum*, *Euonymus*, *Kurrimia*, *Mortonia*, and *Perrottetia*, pits to parenchyma and rays cells similar to the intervacular pitting except in *Kurrimia*, in which they are commonly unilaterally compound or large and elongated. 'Fibriform vessel members' reported (1886) in *Euonymus* and *Pachystima*. Mean member length 0.6–1.0 mm. **Parenchyma** typically apotracheal or absent; diffuse in *Denhamia*, *Maytenus* p.p., *Myginda* (Fig. 90 E), *Rhacoma*, *Schaefferia*,² and *Wimmeria*, in regular multiseriate bands, frequently up to 4 or more cells wide, in *Celastrus* p.p. (Fig. 90 A), *Elaeodendron* p.p., *Gymnosporia* p.p., *Kookoona*, *Lophopetalum* (bands 1–2 cells wide), *Maytenus* p.p., *Pleurostyli*, *Pterocelastrus*, and *Torrabasia*; with similar bands, but composed of septate fibres instead of parenchyma, in several genera (see below under 'Fibres'); parenchyma absent from or very sparse in *Austroplenckia*

¹ With simple perforation in a single species of *Perrottetia* from New Guinea.

² Record and Garratt (1884) describe the parenchyma in *Schaefferia frutescens* Jacquin as 'apparently absent'.

(1886), *Caryospermum* (1154), *Celastrus* p.p. (1886), *Elaeodendron* p.p., *Euonymus*, *Maytenus* p.p., *Mortonia*, *Pachystima* (1886), and *Siphonodon*; vasicentric in *Perrottetia*; transitional between aliform and narrow bands in *Kurrimia* (Fig. 90 I). Seldom containing crystals. Strands usually of up to 4 or 8 cells.

Rays exclusively or predominantly uniseriate in *Austroplenckia* (1886), *Euonymus*, *Hartogia*, *Kookoona*, *Lophopetalum*; some rays up to 2 cells wide in *Maurocenia*, *Microtropis* (1886), *Mortonia*, *Myginda*, *Pachystima* (1853), *Perrottetia*, *Rhacoma*, *Torralbasia*, and *Wimmeria*; usually 3–6 cells wide in the other genera, but sometimes more in species of *Celastrus* and occasionally only 2 cells wide in *Plenckia*; Janssonius (1154) classes the rays as of 2 distinct sizes in some species of *Caryospermum*, *Elaeodendron*, *Microtropis*, and *Siphonodon*; commonly about 1 mm. in height and slightly exceeding this in some species; species with multiseriate rays also have numerous uniseriate rays composed wholly of upright cells; uniseriate rays only 1 or 2 cells high common in *Celastrus* p.p., *Elaeodendron* p.p., *Gymnosporia*, *Maurocenia*, and *Pterocelastrus* p.p.; uniseriate rays rare in *Celastrus* p.p., *Kurrimia*, and *Maytenus* p.p.; more than 12 rays per mm. in most species and up to 20 or more per mm. in *Kookoona*, *Plenckia*, and *Pterocelastrus*; fewer than 12 per mm. in some species of *Kurrimia*, *Maytenus*, and *Siphonodon*; homogeneous (Kribs's Type III), and with rounded cells (tang. section) and conspicuous intercellular spaces in the woods with exclusively uniseriate rays, except in *Hartogia* (heterogeneous Type III); similar, but less marked, intercellular spaces present also in *Maurocenia*, *Maytenus* p.p., and *Pleurostylia*; distinctly heterogeneous (Kribs's Types I and II A) in the genera with multiseriate rays, with 4 or more marginal rows of upright cells except in *Denhamia*, *Maytenus* p.p., *Mortonia*, *Pterocelastrus* p.p., and *Wimmeria*, and commonly with 10 or more rows in some species of *Cassine*, *Catha*, *Elaeodendron*, *Gymnosporia*, *Rhacoma*, and *Siphonodon*; groups of multiseriate procumbent cells sometimes alternating with, and not much wider than, the uniseriate upright cells, e.g. in *Catha*, *Elaeodendron* p.p., and *Pleurostylia*. Single crystals occur in the ordinary cells of most species and large crystals in idioblasts occur in *Siphonodon celastrineus* Griff.; dark deposits present in some species. **Fibres** of most species with numerous, distinctly bordered pits on all walls, the borders often very large, but rather smaller in *Gymnosporia* p.p.; borders absent from or very indistinct in *Perrottetia* and *Siphonodon*; with occasional septa in *Euonymus*; septate fibres with simple, slit-like pits, form the ground tissue in *Caryospermum* (1154) and *Siphonodon* and multiseriate bands of septate fibres occur among the fibre-tracheids in *Cassine*, *Catha*, *Celastrus* p.p., *Elaeodendron* p.p., *Fraunhoferia* (2158), *Gymnosporia* p.p., *Hartogia*, *Maurocenia*, *Maytenus* p.p., and *Plenckia*; these bands of septate fibres are exactly comparable in distribution with the multiseriate bands of parenchyma occurring in other species (cf. A and G in Fig. 90), and in a single genus the bands may be composed of septate fibres in one species and of parenchyma in another; with spiral thickening in *Euonymus*, except *E. javanicus* Blume, and very occasionally in *Pachystima* (Record 1853), walls varying from thin, e.g. most species of *Lophopetalum*, to extremely thick, e.g. *Kurrimia* and *Pterocelastrus*; mean length 0.8–1.8 mm. Vasicentric **tracheids** present in *Microtropis bivalvis* Wall. (1154).

ROOT

Structure described by Colas (446) for *Maytenus* sp. as follows: Cork consisting of 12–15 layers of sub-hexagonal cells. Phelloderm well developed, containing sclerotic idioblasts. Phloem, in transverse sections, appearing as elongated conical groups of rounded cells and sieve tubes separated by triseriate rays. Hexagonal fibres also present towards the centre. Xylem consisting of rounded or sub-hexagonal vessels, irregularly distributed in lignified parenchyma. Vessels frequently containing tyloses. Ground tissue of older roots stratified into zones of lignified parenchyma, alternating with hexagonal fibres. Tannin abundant in the tissues. The root structure in species of *Cassine*, *Celastrus*, *Elaeodendron*, *Euonymus*, and *Maytenus* has been described by Weber (2380).

ANOMALOUS STRUCTURE

Excentric growth in thickness recorded in the stem and root of certain species of *Maytenus*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

It was pointed out by Dunn (617) that *Kurrimia*, *Perrottetia*, and *Tripterygium* differ considerably from one another and also from the remainder of the Celastraceae. This distinction is reflected to some extent in the anatomical structure. Dunn also drew attention to the lack of taxonomic agreement between *Dipentodon* and *Goupia*, both of which were included amongst the Celastraceae in the Bentham and Hooker system, and the remainder of the family. In discussing the taxonomic positions to which these genera should be assigned, Dr. T. A. Sprague has expressed the view (not published) that there is no reason for excluding *Tripterygium* from the Celastraceae so far as external morphology is concerned. He points out that it is the type genus of Loesner's (1389) sub-family Tripterygioideae. Very little is known at present concerning the anatomy of the other genera included in this sub-family. In Dr. Sprague's opinion *Perrottetia* and *Kurrimia* are not sufficiently distinct for them to be excluded from the Celastraceae. *Goupia*, on the other hand, is more definitely aberrant, and has been described in this book under the distinct family Goupiaceae, while *Dipentodon* has been dealt with under Flacourtiaceae. For further views concerning *Goupia* see p. 398.

(ii) FROM WOOD STRUCTURE

The wood anatomy seems to bear little relation to the sub-families and the whole family appears to be rather heterogeneous. Broad bands of either parenchyma or septate fibres are a characteristic feature of *Cassine*, *Catha*, *Celastrus*, *Elaeodendron*, *Gymnosporia*, *Hartogia*, *Kookoona*, *Lophopetalum*, *Maurocenia*, *Maytenus*, *Plenckia*, *Pleurostylia*, *Pterocelastrus*, and *Torralbasia*—a list that is composed mainly of Eucelastreae and Eucassineae. Diffuse parenchyma is present in *Denhamia*, *Maytenus*, *Myginda*, *Rhacoma*, *Schaefferia*, and *Wimmeria*—i.e. mostly from the same groups but with *Wimmeria* (Tripterygioideae) in addition; parenchyma absent from *Euonymus* and *Mortonia*. This leaves *Caryospermum*, *Kurrimia*, *Perrottetia*, and *Siphonodon* as odd genera with paratracheal parenchyma and without fibre tracheids.

ECONOMIC USES

The root bark of *Euonymus americana* Linn. and *E. atropurpurea* Jacq., which was at one time reputed to possess medicinal properties, has been described anatomically by Holm (1035). Members of the same genus have also aroused interest in Russia as a possible source of rubber. An oil with medicinal properties is obtained from the seeds of *Celastrus paniculata* Willd. According to Colas (446) the medicinal bark of *Maytenus chuchuasha* R. H. et R. Colas from the Amazon region exhibits the following anatomical characters. Cork consisting of 7–8 rows of cells with thin, sinuous, suberized walls, and the phelloderm of 10–12 rows of cells. Region below the phelloderm including numerous sclerotic cells. Phloem arranged in tangentially elongated strands, separated by rays 1–3 cells wide, and differentiated into the following concentric zones: (i) The innermost consisting of polygonal cells arranged in radial rows. (ii) The second somewhat collenchymatous, consisting of rounded elements in radial rows, with sieve tubes present amongst them, the whole zone being stratified by strands of hexagonal fibres with small lumina. (iii) The third zone similar in structure to the innermost one, but cells more collenchymatous. (iv) The fourth zone composed of radially elongated bands of phloem tissue, consisting of collenchymatous elements accompanied by radial bands of regularly arranged fibres, separated by large ovoid cells. Pyramidal crystals and tanniniferous cells present, the latter chiefly in the region between the cork and the cones of phloem elements.

Arabian or African tea, which consists of the leaves and twigs of *Catha edulis* Forsk., exhibits the following leaf structure. Cuticle on both surfaces very thick. Epidermal cells from both surfaces with somewhat sinuous anticlinal walls. Stomata confined to the lower surface, surrounded by 3–5 ordinary epidermal cells. Palisade tissue consisting of 1–3 layers in different specimens. Spongy mesophyll often occupying more than half the width of the lamina. Tanniniferous cells, with yellowish-brown contents, scattered throughout the lamina, but particularly numerous in the cortical region and phloem of the midrib. Cluster crystals present with varying frequency in the mesophyll and epidermis. Vascular bundles of the smaller veins accompanied by thick-walled fibres, especially on the lower side. Vascular strand of the midrib, in transverse sections, appearing arc-shaped with incurved ends, and accompanied by a broad band of thick-walled fibres on the abaxial side. Smaller subsidiary strands with similar structure sometimes present in the midrib as well. Petiole with abundant tanniniferous cells in the cortex, and supplied by a crescent-shaped vascular strand; pericyclic sclerenchyma poorly developed (Fig. 88 G).

Few of the species of this family are large enough to produce timber, but two species of *Lophopetalum* furnish soft, even-textured, and easily worked timbers that are used in India, and some species of *Maytenus* are used locally in South America. Some of the smaller trees and shrubs produce dense woods that are used locally as boxwood substitutes and the wood of *Euonymus* spp. is used for 'orange' manicure sticks and for small articles of turnery.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Cassine,* Catha,* Celastrus,* Denhamia, Elaeodendron,* Euonymus,*
 Fraunhofer, Glossopetalon, Glyptopetalum, Gyminda, Gymnosporia,
 Kokoona, Kurrimia,* Lauridia, Lophopetalum, Maurocenia, Maytenus,
 Microtropis,* Mortonia, Myginda, Mystroxydon, Pachystima, Perrottetia,*
 Plenckia, Pleurostylium, Polycardia, Pterocelastrus, Putterlickia, Rhacoma,
 Schaefferia, Siphonodon, Tripterygium,* Wimmeria, Zinowiewia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Austroplenckia, Caryospermum, Cassine, Catha, Celastrus, Denhamia,
 Elaeodendron, Euonymus, Gymnosporia, Hartogia, Kokoona, Lophope-
 talum, Maurocenia, Maytenus, (Microtropis), Mortonia, Myginda, (Othero-
 dendron), (Pachystima), Perrottetia, Plenckia, Pleurostylium, Pterocelastrus,
 Rhacoma, Schaefferia, Siphonodon, Torralbasia, (Tripterygium), Wimmeria.

LITERATURE

(i) *On General Anatomy*

Beauvisage 163, Colas 446, Dunn 617, Holm 1035, Loesner 1389, Rehfoos 1904,
 Sabnis 1977, Weber, W. 2380.

(ii) *On Wood Structure*

Benoist 170, den Berger 182, Besson 186, Burgerstein 312, Chalk and Chattaway 358,
 Desch 574, Greguss 2522, Janssonius 1147, 1154, Jolly 1188, Kanehira 1206, 1209,
 Martin-Levigne 1450, McNair, G. T. 1472, Méniard 1492, Pearson and Brown 1679,
 Pfeiffer, H. 1712, Pfeiffer, J. Ph. 1713, Record 1783, 1800, 1843, 1851, 1853, 1884,
 Record and Hess 1886, Record and Mell 1894, Stone 2202, 2207, Tang 2231, Yamabayashi
 2478.

96. GOUPIACEAE

(FIG. 88 on p. 382; FIG. 89 on p. 388)

SUMMARY

Small to very large trees belonging to the single genus *Goupia* which occurs
 in the Amazon region, Colombia, &c. An interesting anatomical character is
 the complex vascular structure of the **petiole**. The wood exhibits the follow-
 ing features. **Vessels** medium-sized and solitary, perforation plates scalari-
 form, pits to parenchyma small, often with coalescent apertures and uni-
 laterally compound, members very long. **Parenchyma** apotracheal, scattered
 among the fibres, and paratracheal, vasicentric to aliform. **Rays** 2-5 cells
 wide; markedly heterogeneous, relatively small multiseriate groups of pro-
 cumbent cells often separated by many uniseriate upright cells. **Fibres** with
 bordered pits, moderately to very long. **Vasicentric** tracheids present.

LEAF

Dorsiventral. **Hairs** sparse, consisting of short, unicellular trichomes with
 relatively thick walls. **Epidermis** on the upper surface consisting of several
 layers of cells separated by thin walls; cells of the outer epidermal layer on
 both surfaces polygonal, with almost straight but slightly thickened and pitted
 anticlinal walls. **Stomata** confined to the lower surface, each surrounded by
 about 4 epidermal cells, not very clearly differentiated from those of the

remainder of the epidermis (ranunculaceous). **Mesophyll** composed of about 2 layers of palisade tissue, and a broader spongy region; containing branched sclerenchymatous elements (idioblasts). Vascular bundles of the smaller **veins** embedded in the mesophyll; larger veins with cylindrical xylem accompanied by small phloem groups, the whole being surrounded by a broad ring of fibres. Main vascular strand of the **petiole** (Fig. 88 A) appearing, in transverse sections through the distal end, as an abaxial arc of xylem and phloem, accompanied by an arc of closely placed bundles on the adaxial side, the whole strand resembling an almost closed circle surrounding about 4 medullary bundles and accompanied externally by cortical strands. Cortical region of the petiole containing tanniniferous cells. Cluster **crystals** observed.

AXIS

YOUNG STEM

Cork superficial in material examined at Kew. **Cortex** narrow. **Pericycle** containing a composite and continuous ring of sclerenchyma. **Xylem** with numerous, evenly distributed, mostly solitary vessels, up to about 100 μ in radial diameter, with scalariform perforation plates. **Pith** small, quadrangular, somewhat heterogeneous, including cells with lignified pitted walls and others with granular contents. Cluster **crystals** observed.

WOOD (Fig. 89 H-L)

Vessels medium-sized (100–200 μ mean tangential diameter) or slightly larger; exclusively solitary; about 10 per sq. mm. Perforation plates scalariform with 3–10 thick bars. Intervascular pitting very rare, pits to ray and wood parenchyma small and often with coalescent apertures, sometimes unilaterally compound, several pits subtending a narrow, elongated pit in the parenchyma wall, particularly in the wood parenchyma cells, such pits horizontal, vertical, or oblique. Solid deposits moderately common. Mean member length about 1.7 mm. **Parenchyma** scattered among the fibres and associated with the vessels, the latter varying from a few cells on the abaxial sides to complete sheaths, and often forming distinct, narrow wings (Fig. 89 H). Strands composed of 8 or more cells. **Rays** 2–5 cells wide and commonly more than 1 mm. high; uniseriate only moderately numerous, composed of high upright cells; about 14 rays per mm.; markedly heterogeneous (Kribs's Type I), and consisting of 2 or 3 multiseriate portions of procumbent cells separated by several rows of uniseriate upright cells (Fig. 89 L); the biseriate parts scarcely any wider tangentially than the uniseriate parts; with occasional sheath cells in the larger rays; sometimes with occasional solitary crystals in the upright cells. **Fibres** with numerous distinctly bordered pits on both radial and tangential walls, the borders larger than those of the intervacular pitting; walls very thick; mean length about 2.2 mm. **Vasicentric tracheids** present.

TAXONOMIC NOTES

Goupia was included in the Celastraceae in the Bentham and Hooker system, but was given the status of a sub-family Goupioideae within the Celastraceae by Loesner (1939). In Dr. T. A. Sprague's opinion the genus should be restored to the status of a family as recommended by Miers (1916 A). Dr. Sprague has pointed out (unpublished) that the venation of the leaves, the

stipules, the aestivation of the petals, the anthers, and the gynoecium are highly characteristic and taken together are sufficient to exclude *Goupia* from the Celastraceae. For these reasons, together with the petiolar structure, which is unlike that of the Celastraceae (with the possible exception of *Kurrimia* and *Lophopetalum*), *Goupia* has been treated as a separate family in this book. The wood is of an unspecialized type.

ECONOMIC USES

Goupia glabra Aubl. in British Guiana produces a strong, durable timber suitable for heavy construction.

GENUS DESCRIBED

The above description of the general anatomy is based on an examination of *Goupia glabra* Aubl.* in the Kew herbarium.

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Loesner 1389, Miers 1516 A.

(ii) *On Wood Structure*

Janssonius 1154, Méniard 1491, Record 1853, Record and Hess 1886, Record and Mell 1894.

97. HIPPOCRATEACEAE

(FIG. 88 on p. 382; FIG. 89 on p. 388; FIG. 91 on p. 402)

SUMMARY

(i) GENERAL

A tropical family of small trees or shrubs, sometimes scandent. The anatomical characters are very similar to those of the Celastraceae. One of the most characteristic features is the occurrence of **laticiferous canals** which are confined to the axis of some species, but occur in the leaf as well in others. Some of the mesophyll cells also contain a material resembling rubber. Although laticiferous elements are so characteristic of the family they are not always easily seen, especially if the contents have been dissolved when preparing and mounting the sections. **Sclerosed cells** of various kinds are common in the leaf. The **petiole** structure exhibits a considerable range of variation in different species (see 'Leaf'). **Anomalous thickening** has been recorded in *Salacia*.

(ii) WOOD

Vessels medium-sized to large, usually solitary, perforations simple, pits to parenchyma usually small; members of medium length. **Parenchyma** paratracheal, rather sparse. **Rays** exclusively uniseriate or of 2 distinct sizes, the larger up to 30 cells wide and very high. **Fibres** of 2 types, those of the ground tissue with bordered pits and thick walls; scattered amongst these are thin-walled septate fibres with various parenchyma-like distributions, moderately short. **Included phloem** of the foraminate, concentric or interrupted type present in several species.

LEAF

Generally dorsiventral; rarely centric in *Hippocratea* and *Salacia*. **Hairs** stellate, with uniseriate rays in *Hippocratea velutina* Afzel.; uniseriate, but with closely placed septa at the base in *H. iotricha* Loes.; unicellular, papillose in *H. aspera* Lam. **Cork warts** present on the lower surface in certain species of *Salacia*. **Epidermis** containing crystal cells (idioblasts) in most species of *Hippocratea* and *Salacia*. Outer walls of the epidermal cells stated to be pitted in *Salacia oblonga* Wall. **Stomata** usually confined to the lower surface, but exceptions recorded in a few species of *Campylostemon* and *Hippocratea*; mostly ranunculaceous, but instances recorded in all 3 genera of the guard cells being surrounded by 1 or 2 (*Salacia dulcis* Benth.) circles of 4 cells each, 2 cells in each ring being parallel to the pore. **Hypoderm** of 1 or 2 layers common below the upper surface of the leaf in *Campylostemon*, *Hippocratea*, and *Salacia*. Some of the mesophyll cells contain deposits of a rubber-like substance. **Mesophyll** including various types of sclerosed cells, such as the 'spicular cells', connected with the sclerenchyma of the veins in species of *Salacia*. Vascular system of the **petiole** very variable, exhibiting the following types of structure in transverse sections. (i) A horseshoe-shaped group of bundles in some species of *Hippocratea* and *Salacia*. (ii) A ring of bundles surrounding an inversely orientated plate of xylem and phloem in *S. micrantha* Peyr. (iii) An arc-shaped strand towards the abaxial side, but having an adaxial plate of xylem and phloem partly surrounded by the arc in *S. roxburghii* Wall. (Fig. 88 c). (iv) With a flattened ring of bundles accompanied on the upper side by 3 or 4 inversely orientated bundles in *S. crassifolia* Peyr. **Tanniniferous cells** occur in the mesophyll of species of *Hippocratea* and *Salacia*. Large **secretory cavities** present in the cortical tissue of the petiole and in the margins of the lamina of *S. roxburghii*. **Laticiferous canals** (see also 'Axis') have been recorded in species of *Hippocratea* and *Salacia* as well as in one of *Campylostemon* where they accompany the phloem of the veins and usually extend into the mesophyll. Mesophyll also containing mucilage cells in *Hippocratea velutina* Afz. Solitary and clustered **crystals** common; see also under 'Epidermis'.

AXIS

YOUNG STEM

Cork arising in the second to the fourth layer of the cortex. Cork cells with fairly wide lumina; often thin walled or with strong thickening of the inner or outer tangential walls. Primary **cortex** frequently including branched stone cells, especially in the inner portion. **Pericycle** with isolated strands of fibres in some species, or a composite and continuous ring of sclerenchyma in others. **Phloem** containing fibres and branched sclerenchymatous cells. **Xylem** usually including vessels with simple perforations; scalariform plates also recorded in 1 species of *Salacia*. **Pith** sometimes containing stone cells. **Laticiferous canals** (see also under 'Leaf') recorded in species of *Hippocratea* and *Salacia* and in one of *Campylostemon*; generally situated in the phloem, or, more rarely, in the primary cortex. Phloem also containing tannin sacs in *Hippocratea* and *Salacia*. Solitary and clustered **crystals** common, solitary ones sometimes very abundant. Solitary crystals in the cortex and pith much larger than those in the phloem in *Salacia roxburghii* Wall.

BARK

Bark in many members of the family stated by Loesner (1390) to contain a reddish-yellow pigment, soluble in alcohol.

WOOD (Fig. 89 I, J, and M, Fig. 91 C)

Vessels medium-sized (100–200 μ mean tangential diameter) in *Cheiloclinium* and *Salacia*, large (more than 200 μ) in *Hippocratea* in the material examined, but reported by Record (1853) to be minute in some species; exclusively solitary or almost so, except in *Pristimera* (1886); very variable in number even in different areas of the same stem, average about 10–16 per sq. mm. Perforations simple; intervacular pitting rare, pits to parenchyma small, often with striations due to coalescent, slit-like apertures, sometimes unilaterally compound or horizontally elongated in *Hippocratea*. Tyloses not observed; gum present in some species of *Salacia*. Mean member length 0.5–0.7 mm. **Parenchyma** exclusively paratracheal, as a few cells round the vessels; strands of 4–12 cells. **Rays** in *Cheiloclinium* p.p. and *Salacia* exclusively uniseriate, about 20 per mm. and composed entirely of square or upright cells (Kribs's Heterogeneous Type III); of 2 distinct sizes in *Cuervea* and *Hippocratea*, the larger up to 30 cells wide and of indeterminate height, the smaller rays uniseriate; about 6–10 rays per mm., heterogeneous (Kribs's Type II A). Crystals and gum present in both genera. Record and Hess (1886) note the occurrence of patches of thin-walled cells in some genera. **Fibres** of the ground tissue with conspicuous bordered pits which are usually larger than the intervacular pitting and equally numerous on both radial and tangential walls; interspersed among these fibres, with a parenchyma-like distribution, are thin-walled septate fibres with simple or inconspicuously bordered pits; as scattered cells or short uniseriate lines comparable with diffuse parenchyma in *Cuervea* and *Hippocratea*, aliform to confluent in *Cheiloclinium* and *Salacia*; these cells may be abundant particularly in the first-formed rings of secondary wood (362). Mean length 0.6–0.9 mm. In *Cheiloclinium* and *Salacia* the fibre-tracheids round the vessels have wider lumina and very numerous pits and grade into vasicentric tracheids. **Vasicentric tracheids** usually present. **Included (interxylary) phloem** of the concentric type (*c. l. circumvallatum*) occurs in *Cheiloclinium gleasonianum* A. C. Sm. (1886) and *Salacia* (Fig. 91 C), with successive layers of xylem and phloem separated by broad bands of conjunctive parenchyma containing circular or irregular groups of stone cells; the xylem and phloem layers are only rarely interrupted by interfascicular rays. Record and Hess (1886) report anomalous structure of the 'foraminate' type (*c. l. foraminulatum*) in *Cheiloclinium cognatum* (Miers) A. C. Sm. and *Prionostemma aspera* (Lam.) Miers. Anomalous structure of the 'interrupted' type (*c. l. interruptum*) reported (1853) in *Hippocratea*, 'the breaking of the cambial ring into several arcs results in the formation of unequal amounts of xylem and phloem, and the stem becomes more or less deeply grooved'; with a tendency to such formation also in *Hemiangium* (1886).

ANOMALOUS STRUCTURE

Successive rings of interxylary phloem recorded in *Salacia* (Fig. 91 C). For further details see preceding paragraph.

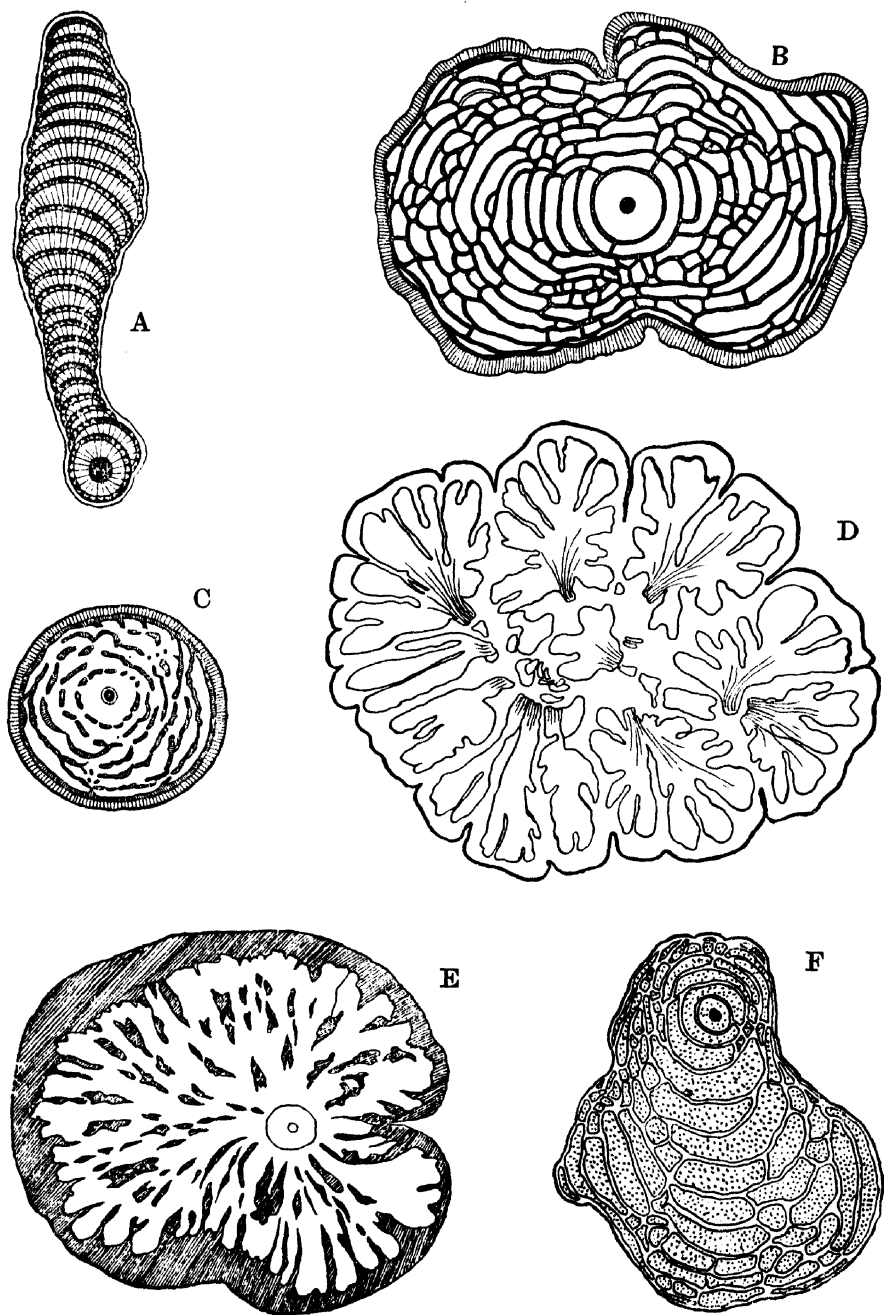


FIG. 91. MENISPERMACEAE, A; POLYGALACEAE, B; HIPPOCRATEACEAE, C; MALPIGHIACEAE, D; APOCYNACEAE, E; CONVULVULACEAE, F

Anomalous stems. A, *Anomosperrum grandisfolium* Eichl. B, *Securidaca lanceolata* St. Hil. Xylem white; phloem and cortex shaded; nat. size. C, *Salacia serrata* Camb. $\times 1\frac{1}{2}$. D, *Tetrapteris* sp. showing split xylem (Schenck Holzss. 500 Rio) nat. size. E, *Condylocarpus* sp. Cortex and interxylary phloem shaded; pith and perimedullary xylem indicated by circles. F, *Porana volubilis* Burm. nat. size. E, After Fritz Müller. Remainder after H. Schenck.

TAXONOMIC NOTES

The general similarity of the anatomical characters to those of a majority of the Celastraceae indicates that the two families are closely related to one another. It is noteworthy that the unusual parenchyma-like distribution of septate fibres in the xylem of the Hippocrateaceae has a parallel in the Celastraceae. This close relationship seems to be supported also by the evidence of external morphology. Smith and Bailey (2141), in discussing the genus *Brassiantha*, have pointed out that the division between the Hippocrateaceae and Celastraceae is artificial.

ECONOMIC USES

According to Colas (446) one or more species of *Salacia* with medicinal properties occur in the Amazon region. No anatomical details are given by Colas.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Campylostemon, Hippocratea, *Salacia*.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Cheiloclinium, Cuervea, (Hemiangium), Hippocratea, (Pristimera), *Salacia*.

LITERATURE

(i) *On General Anatomy*

Colas 446, Loesner 1390, Smith, A. C. and Bailey 2141.

(ii) *On Wood Structure*

Chalk and Chattaway 362, Record 1851, 1853, Record and Hess 1886, Williams 2430.

98. STACKHOUSIACEAE

SUMMARY

A small family of herbs with woody rhizomes comprised in the two genera *Macgregoria* and *Stackhousia* which occur chiefly in Australia, New Zealand, &c. **Tanniniferous cells** occur in the parenchymatous tissues of both leaf and stem. Deposits of a rubber-like substance have been reported, but according to Solereder these are probably fat bodies. It is interesting to note that **crystals** of calcium oxalate have not been observed in the family.

LEAF

Dorsiventral or centric. **Hairs** unicellular. **Stomata** in *Stackhousia spathulata* Sieb. present on both surfaces; ranunculaceous. **Mesophyll** containing tanniniferous cells in *Stackhousia brunonis* (Endl.) Benth. Bodies, variously interpreted as consisting of fat or rubber, also occur in the leaf. Vascular bundles of the **veins**, not accompanied by sclerenchyma.

AXIS

YOUNG STEM

Hypoderm usually well defined. Outer part of the **cortex** containing abundantly pitted fibres in positions corresponding to ribs on the surface of

the stem in all species of *Stackhousia* except *S. pulvinaris* F. v. M. as well as in *Macgregoria*. **Endodermis** frequently composed of large, conspicuous cells. **Pericycle** usually containing isolated bundles of fibres, but sclerenchyma is lacking in *S. maideni* Pampan. and *S. pulvinaris*. **Xylem** containing vessels with simple perforations, a small amount of parenchyma, fibres with bordered pits; rays stated to be absent (cf. woody species of *Veronica*). **Pith** composed of large parenchymatous cells. **Tanniniferous cells** common in the cortex.

RHIZOME

Secretory cells, having wide lumina filled with dark-brown contents, either solitary or in longitudinal rows of a few together, recorded in the phloem.

TAXONOMIC NOTES

The Stackhousiaceae are generally regarded as having affinities with the Celastraceae. If the presence of rubber-like deposits in the Stackhousiaceae could be more definitely established this would provide additional evidence of the affinities of the family since rubber-like substances occur also in the Celastraceae.

GENERA DESCRIBED

Macgregoria, *Stackhousia*.

The above description is largely based on the one previously given by Solereder.

99. RHAMNACEAE

(FIG. 92 on p. 408; FIG. 93 on p. 412)

SUMMARY

(i) GENERAL

This family occurs in both tropical and temperate regions. It consists mainly of trees and shrubs, but includes a few typical xerophytic shrubs such as *Colletia armata* Miers and *Discaria toumatou* Raoul. with flattened, spiny, assimilatory stems and reduced leaves. The family exhibits but few distinctive diagnostic characters, but the following points are worthy of note. The usually mucilaginous **epidermis** of the leaf is papillose in numerous genera. The **stomata** are generally ranunculaceous, but occasionally rubiaceous. The **mesophyll** is usually dorsiventral, but rarely centric. Both solitary and clustered **crystals** occur, whilst acicular ones are characteristic of a few genera; the crystals sometimes appear as transparent dots in the leaf. **Mucilage cells** are common in the leaf and in the primary cortex of the axis, whilst mucilage cavities are sometimes present as well in the latter. Other secretory cells with tanniniferous contents are also frequent. The **petiole**, in transverse sections, usually exhibits a solitary arc-shaped vascular strand, or, more rarely, an arc of separate bundles.

(ii) WOOD

Vessels mostly small, but large in a few species, commonly in multiples

and with a tendency to a radial arrangement, with pronounced 'flames' in some species, ring-porous and with spiral thickening of the late wood vessels in several genera, perforation plates simple, intervacular pitting alternate, with minute to large borders; members of medium length to moderately short. **Parenchyma** predominantly paratracheal in most species, vasicentric, aliform or confluent, predominantly apotracheal or intermediate in a few species. **Rays** mostly 2-5 cells wide but considerably wider in some species and exclusively uniseriate in others, varying from markedly heterogeneous to homogeneous with few uniseriate rays, sometimes composed entirely of square to upright cells. **Fibres** with simple pits; of medium length to moderately short. **Vascular tracheids** present in species with vessels in radial 'flames'.

LEAF

Generally dorsiventral, but sometimes centric or sub-centric. Rolled leaves with a furrow on either side of the median vein occur in *Microrhamnus ericoides* Gray. Furrows formed by the projecting network of veins also occur in species of *Ceanothus* belonging to the sub-genus *Cerastes*. **Hairs** consisting mostly of simple, unicellular or uniseriate trichomes of varying length. Stellate hairs recorded in the Australian genera *Cryptandra*, *Pomaderris*, *Spyridium*, *Trymalium*. **Leaf teeth** sometimes glandular in *Ceanothus*, *Noltea*, *Rhamnus*. **Epidermis** mucilaginous or containing mucilaginous cells in species of *Alphitonia*, *Berchemia*, *Ceanothus*, *Colletia*, *Colubrina*, *Condalia*, *Cormonema*, *Crumenaria*, *Cryptandra*, *Dallachya*, *Discaria*, *Emmenosperma*, *Gouania*, *Hovenia*, *Lamellisepalum*, *Lasiodiscus*, *Maesopsis*, *Paliurus*, *Pomaderris*, *Reissekia*, *Reynosia*, *Rhamnella*, *Rhamnidium*, *Rhamnus*, *Sageretia*, *Scutia*, *Trevoa*, *Trymalium*, *Ventilago*, *Zizyphus*. A double epidermis recorded in a few species of *Ceanothus* and *Rhamnus*. Epidermis, especially on the lower surface of the leaf, provided with papillae in species of *Berchemia*, *Cryptandra* (upper side), *Discaria*, *Helinus*, *Karwinskia*, *Marlothia*. **Stomata** confined to the lower surface in species of *Ceanothus*, *Colletia*, *Gouania*, *Reissekia*, *Rhamnus*, *Ventilago*, *Zizyphus*, but recorded on both sides in *Rhamnus lycioides* Linn.; usually ranunculaceous, but rubiaceous in a few species of *Colletia*, *Rhamnus*, and *Zizyphus*; cruciferous in *Cryptandra* sp. Small crowded stomata recorded in species of *Reynosia* and *Sarcomphalus*, and especially large ones in *Condalia*, *Discaria*, *Emmenosperma*, and *Rhamnus*. **Hypoderm** below the upper epidermis recorded in a few species of *Ceanothus*, *Microrhamnus*, *Rhamnus*, *Sarcomphalus*. **Mesophyll**. Palisade tissue, containing isolated enlarged cells filled with mucilage, present in species of *Condalia* and tanniniferous cells in species of *Condalia*, *Maesopsis*, *Pomaderris*, *Rhamnella*, and *Scutia*, the cells being more or less sclerosed in certain of these genera; mucilage and tannin occur together in *Discaria* and *Talguenea*. Palisade tissue consisting of a single layer composed of broad tanniniferous cells in *Cryptandra oborata* Sieb. Mesophyll consisting wholly of palisade parenchyma in species of *Ceanothus* with furrowed leaves (see above). Spongy mesophyll composed of elongated, interwoven cells in *Reynosia* and *Sarcomphalus*. Idioblasts filled with brown contents sometimes present in *Colletia*, *Scutia*, and species of *Zizyphus* (Sabnis 1977). Small lateral veins vertically transcurrent in species of *Alphitonia*, *Ceanothus*, *Colubrina*, *Cormonema*,

Crumenaria, *Helinus*, *Hovenia*, *Karwinskia*, *Pomaderris*, *Reynosia*, *Rhamnidium*, *Sageretia*, *Sarcomphalus*, *Zizyphus*; veins embedded in the mesophyll in the Colletieae, Gouanieae, and Ventilagineae (of Bentham and Hooker), as well as in *Condalia*, *Emmenosperma*, *Krugiodendron*, *Lasiodiscus*, *Rhamnus*, *Scutia*, *Trymalium*, and species of *Zizyphus*; larger lateral veins accompanied by a sclerenchymatous sheath in the Ventilagineae and also in species of *Berchemia*, *Emmenosperma*, *Gouania*, *Lamellisepalum*, *Lasiodiscus*, *Phyllica*, *Reynosia*, *Sageretia*, *Sarcomphalus*, *Scutia*, and *Zizyphus*. Smaller veins provided with a sheath of large, tanniniferous, parenchymatous cells in *Condalia*, *Krugiodendron*, *Microrhamnus*, *Rhamnus* (especially the section *Cervisporia*), *Zizyphus*. **Petiole**, in transverse sections through the distal end, exhibiting a single open or somewhat U-shaped arc of xylem and phloem in examined species of *Berchemia*, *Ceanothus*, *Discaria*, *Frangula* (Fig. 93 B), *Gouania*, *Noltea*, *Paliurus*, *Pomaderris*, *Zizyphus*. Three separate bundles in the form of an open arc occur in *Discaria serratifolia* (Vent.) Benth. and *Paliurus spinachristi* Mill. (Fig. 93 F), whilst the continuous, open, arc-shaped strand of *Gouania domingensis* Linn. is accompanied by two very small, latero-superior bundles. Large clustered **crystals** recorded in the mesophyll of species of *Colubrina*, *Condalia*, *Cryptandra*, *Hovenia*, *Krugiodendron*, *Lasiodiscus*, *Pomaderris*, *Rhamnus*, *Trevora*, *Trymalium*, and *Zizyphus*. Solitary crystals recorded in enlarged palisade cells in species of *Karwinskia*, *Reynosia*, *Rhamnidium*, *Rhamnus*, *Zizyphus*. Acicular crystals (styloids) abundant in *Gouania*. **Mucilage receptacles** recorded in the parenchyma of the larger leaf veins, and in the petiole in *Alphitonia*, *Berchemia*, *Ceanothus* (pro parte), *Colubrina*, *Condalia* (pro parte), *Cormonema*, *Dallachya*, *Emmenosperma*, *Gouania*, *Hovenia*, *Karwinskia*, *Lasiodiscus*, *Maesopsis*, *Paliurus*, *Rhamnella*, *Rhamnidium*, *Rhamnus* (pro parte), *Ventilago* (pro parte), *Zizyphus*.

Cooper (463) and Chodat (398) have described the leaf structure of various species of *Ceanothus* and *Rhamnus* in some detail. The distribution of crystals and secretory cells, the proportion of palisade tissue in the mesophyll, together with features of the epidermis and stomata were found to provide characters of specific diagnostic value.

AXIS

YOUNG STEM (Fig. 93 A, C, and E)

Cork arising in the epidermis or sub-epidermis in at least certain species of *Ceanothus*, *Discaria*, *Pomaderris*, *Rhamnus*, *Zizyphus*. **Pericycle** containing isolated strands of fibres in species of *Alphitonia*, *Berchemia*, *Ceanothus*, *Colletia*, *Colubrina*, *Condalia*, *Discaria*, *Emmenosperma*, *Gouania*, *Hovenia*, *Noltea*, *Paliurus*, *Phyllica*, *Pomaderris*, *Rhamnus*, *Soutia*, *Ventilago*, *Zizyphus*; a composite and continuous ring of sclerenchyma recorded in other species of *Zizyphus*. Stone cells observed in the pericycle in *Gouania domingensis* Linn. Secondary **phloem** including bands of fibres often sheathed by septate fibres which contain solitary crystals. **Xylem** in all investigated species in the form of a continuous cylinder traversed by narrow rays; including vessels with simple perforations, except for occasional scalariform perforation plates in *Phyllica* and, according to Solereder, in *Zizyphus*. Wood fibres with simple pits. **Secretory cells**, usually filled with mucilage or tanniniferous materials, occur in all unglified tissues of the stem, but their distribution varies

slightly in different species. Elongated **secretory cavities** also present in the cortex and pith of *Frangula alnus* Mill. (syn. *Rhamnus frangula* Linn., Fig. 93 E), *R. californica* Eschsch., and *R. purshiana* DC., but they tend to disappear in old material. Solitary and clustered **crystals** common. Solitary forms observed in the cortex in certain species of *Berberis*, *Phylla*, *Zizyphus*, in the phloem of species of *Pomaderris* and *Rhamnus*, in the pith in species of *Ceanothus*, *Colletia*, *Discaria*, *Paliurus*, *Pomaderris*. Clustered crystals observed in the cortex in species of *Ceanothus*, *Colletia*, *Discaria*, *Pomaderris*, *Rhamnus*, *Zizyphus*, in the phloem in species of *Ceanothus*, *Discaria*, *Pomaderris*, *Rhamnus*, *Zizyphus*, and in the pith in species of *Ceanothus*, *Discaria*, *Pomaderris*, *Rhamnus*. The occurrence and distribution of crystals are of specific rather than generic diagnostic value.

The **assimilatory stems** of *Colletia armata* Miers and *Discaria toumatou* Raoul possess a very thick cuticle, numerous stomata, a well-defined hypoderm, several layers of palisade chlorenchyma in the outer part of the cortex, whilst large solitary crystals occur in the medullary rays and in the perimedullary region.

BARK

The anatomy of the bark of *Ceanothus* and *Rhamnus* has been described for species with medicinal properties. Further particulars are given below under 'Economic Uses'.

WOOD (Fig. 92)

Vessels mostly small (less than 100 μ mean tangential diameter), very small in *Auerodendron*, *Berberis*, *Ceanothus* p.p., *Colletia*, *Discaria*, *Krugiodendron*, *Lasiodiscus*, *Reynosia*, and *Rhamnus*, medium-sized in *Ampeloxizyphus*, *Colubrina* p.p., *Hovenia*, and *Maesopsis*, and large in *Ventilago*; never exclusively solitary, multiples of 4 or more cells moderately common in *Krugiodendron*, *Lasiodiscus*, *Pomaderris*, *Rhamnus* p.p., and *Ventilago*, and in pronounced radial or oblique flames (Fig. 92 A and H) in *Ceanothus* p.p., *Condalia*, *Microrhamnus*, and *Rhamnus* p.p., and similar or almost ulmiform (Fig. 92 K) in *Colletia* and *Discaria*, with a tendency to radial or oblique arrangement in *Auerodendron*, *Ceanothus incanus* T. et G., and *Rhamnella*; very numerous in woods with radial flames, varying from 6 to 60 per mm. in the woods with small vessels and from 2 to 7 per mm. in those with medium-sized or large vessels, most numerous (apart from woods with radial 'flames') in *Krugiodendron* and *Lasiodiscus* (more than 30 per mm.) and fewest (2-4 per mm.) in *Hovenia*, *Maesopsis*, and *Ventilago*; ring-porous or semi-ring-porous in *Ceanothus* p.p., *Colletia*, *Condalia* p.p., *Discaria* (Record 1856), *Hovenia*, *Rhamnella*, *Rhamnus*, and *Zizyphus* p.p. (Record 1851); with spiral thickening in *Adolia* (Record 1783), *Ceanothus*, *Colletia*, *Colubrina* (1868), *Condalia*, *Discaria* p.p., *Doerpfeldia* (1868), *Microrhamnus*, *Rhamnus*, *Sarcophalus* (1868), *Scutia*, and *Zizyphus jujuba* Mill. (2158). Perforation plates exclusively simple, except that Solereder records some scalariform plates with few bars in *Phylla* and *Zizyphus calophylla* Wall. Intervascular pitting alternate, with coalescent apertures in many species, sometimes very marked, as in *Hovenia* and *Paliurus*; pits small to minute in *Auerodendron*, *Krugiodendron*, *Lasiodiscus*, *Paliurus*, *Pomaderris*, *Reynosia*, *Rhamnella*, *Sageretia*,

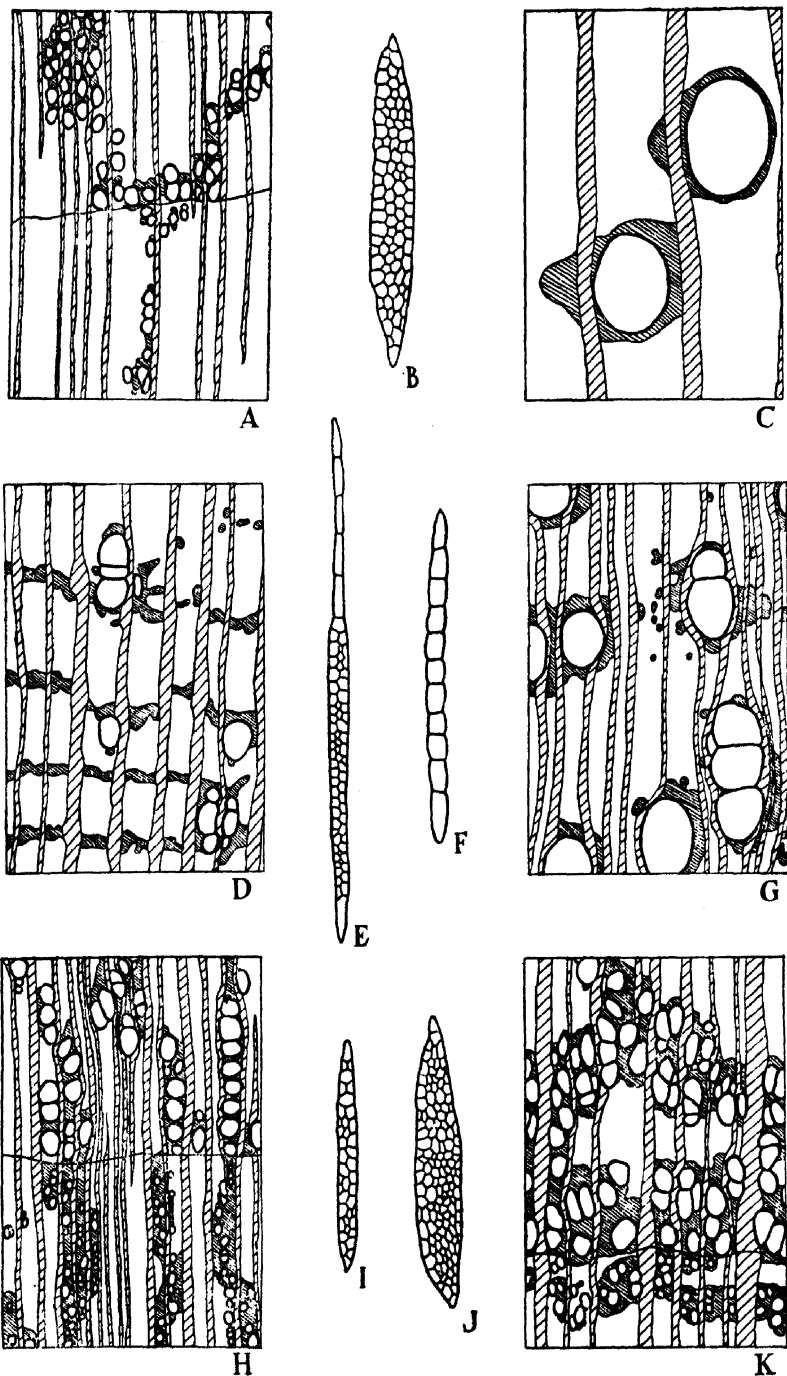


FIG. 92. RHAMNACEAE

A, *Rhamnus cathartica* Linn. B, *Maesopsis eminii* Engl. C, *M. eminii* Engl. D, *Doerpfeldia cubensis* Urb. E, *Colubrina panamensis* Standl. F, *Zizyphus jujuba* Lam. G, *Z. jujuba* Lam. H, *Ceanothus incanus* T. et G. I, *C. thyrsiflorus* Esch. J, *Colletia discolor* Hook. f. K, *C. discolor* Hook. f.

and *Scutia*, moderately large to large in the other genera; pits to parenchyma and ray cells similar to the intervacular pitting, occasionally unilaterally compound. Tyloses not observed but recorded by Kanehira (1206) for *Paliurus samosissimus* Poir.; solid deposits present in some species and abundant in *Reynosia* (Record 1856). Mean member length 0.3–0.7 mm. **Parenchyma** very sparse to moderately abundant, predominantly paratracheal in most species; most commonly as a few cells round the vessels; aliform and sometimes locally confluent in *Auerodendron*, *Colubrina* p.p., *Discaria*, *Maesopsis* (Fig. 92 c), *Reynosia*, *Scutia*, and *Zizyphus* p.p. (Fig. 92 g), confluent in *Doerpfeldia* (Fig. 92 d) and *Zizyphus* p.p.; associated with the vessels where these are in 'flames' but very sparse in *Ceanothus*, *Microrhamnus*, and some species of *Rhamnus*; with some diffuse parenchyma in addition to paratracheal in *Auerodendron* and *Doerpfeldia* and also, according to Kanehira (1206), in *Paliurus ramosissimus* Poir. and two species of *Rhamnus*; in wavy bands, according to Williams (2430), in *Gouania lupuloides* (L.) Urban.; predominantly diffuse in *Sarcomphalus* and some species of *Zizyphus*, e.g. *Z. angolito* Standl.; with uni- to biseriate terminal bands in *Ampelozizyphus*, *Hovenia*, *Lasiodiscus*, *Paliurus*, *Sageretia*, *Sarcomphalus*, *Scutia*, and *Zizyphus* p.p.; in *Zizyphus* the parenchyma is very variable being, for example, predominantly apotracheal in numerous uniseriate bands in *Z. angolito* Standl., *Z. cyclocardia* Blake, *Z. guatemalensis* Hemsl., *Z. hawaensis* H. B. et K., and *Z. sonorensis* S. Wats. (1886), in narrow irregular to broad confluent bands in *Z. melastomoides*, *Z. mistol* Griseb., and *Z. spina-christi* Willd. p.p., aliform in other species, often accompanied by irregularly scattered single strands. Crystals in chambered cells observed in *Auerodendron*, *Berchemia*, *Maesopsis*, and *Rhamnella* and also reported by Record (1856) in some species of *Colletia*, *Colubrina*, *Condalia*, *Doerpfeldia*, *Karwinskia*, *Rhamnidium*, *Sageretia*, and *Sarcomphalus*. Storied in *Ventilago*. Very thin-walled in most of the species. Strands typically of 4 cells, but occasionally up to 6 or 8 cells, e.g. in *Ampelozizyphus*, *Paliurus*, *Rhamnella*, *Rhamnidium*, and *Zizyphus*. Chambered crystals sometimes present. **Rays** most commonly up to 2–5 cells wide, exclusively uniseriate in *Paliurus* and some species of *Zizyphus*, e.g. *Z. jujuba* Mill. and *Z. mucronata* Willd.; up to 6–8 cells wide in *Colletia*, *Discaria* (Record 1856), and *Ventilago* and up to 30 cells wide in *Ampelozizyphus*; of 2 distinct sizes in *Ampelozizyphus* and with relatively few intermediates between uniseriate and 4 or more cells wide in *Ventilago*; less than 1 mm. high except in *Scutia* (up to 1.5 mm.) and *Ampelozizyphus*, in which very high primary rays occur in various stages of dissection into smaller units; uniseriate rays scarce or commonly only 1 or 2 cells high in *Auerodendron*, *Colletia*, *Condalia*, *Maesopsis*, *Rhamnella*, *Rhamnidium*, and *Rhamnus* p.p.; about 10–20 rays per mm. in woods with rays up to 3 cells wide, 4–10 per mm. in woods with larger rays, more numerous in *Sageretia* and *Scutia*, fewest in *Maesopsis*; usually heterogeneous (Kribs's Types II A and B); with 4 or more marginal rows of distinctly upright cells in *Berchemia*, *Colubrina*, *Comonema*, *Emmenosperma*, *Hovenia*, *Karwinskia* (Record 1856), *Lasiodiscus*, *Pomaderris*, *Rhamnidium*, *Sageretia*, and *Zizyphus* p.p.; homogeneous (Kribs's Types I–II) or with a single marginal row of square cells not much higher axially than the procumbent cells in *Maesopsis*, *Rhamnus*, and *Ventilago*, and, according to Record and Hess (1886), in some specimens of *Doerpfeldia* and *Sarcomphalus*;

the other genera intermediate; the shrubby members often with their procumbent cells replaced by square cells or with uniseriate margins of square cells that are not distinguishable from the procumbent cells in tangential sections, e.g. *Ceanothus incanus* T. et G. and *Microrhamnus*; wood with wholly uniseriate rays homogeneous (Kribs's Type III), heterogeneous (Kribs's Type II) or composed entirely of square and upright cells; sheath cells present in *Rhamnella*; cells very commonly containing gum-like deposits and single crystals, the latter very numerous in *Doerpfeldia*, *Krugiodendron*, *Scutia*, and *Zizyphus mucronata* Willd.; with a tendency to arrangement in echelon in *Krugiodendron* and *Maesopsis*. **Fibres** with simple pits, more numerous on the radial than the tangential walls, usually very sparse, but more numerous in some of the woods with thin-walled fibres; often septate, according to Kanehira (1206) in *Rhamnus formosana* Mats. Walls thick to very thick in *Auerodendron*, *Berchemia*, *Ceanothus* p.p., *Colletia*, *Condalia*, *Discaria* (1856), *Doerpfeldia*, *Emmenosperma*, *Krugiodendron*, *Lasiodiscus*, *Paliurus*, *Reynosa*, *Sageretia*, *Scutia*, and *Zizyphus* p.p., thin-walled in *Alphitonia*, *Ampeloxizyphus*, *Ceanothus* p.p., *Colubrina*, *Cormonema*, *Hovenia*, and *Maesopsis*; very commonly with a gelatinous inner layer. Mean length 0.7–1.7 mm. **Vascular tracheids** present in woods with vessels in radial 'flames'; often spirally thickened.

ROOT

Bottomley (241) has described nodules on the roots of *Ceanothus americanus* Linn. which contain nitrogen-fixing bacteria. Root nodules are rare in specimens of *C. americanus* cultivated in Great Britain but common in American specimens. The nodules are stated to increase in size by means of outgrowths of endogenous origin, and, when mature, are differentiated into four distinct zones: (i) An apical meristematic zone. (ii) A zone where the cells become infected with bacteria. (iii) A zone containing enlarged, radially elongated cells filled with bacteria. (iv) A basal zone almost free from bacteria.

Holm (1064) has recorded the occurrence of concentric bands of mechanical tissue surrounding the stele in *Rhamnus purshiana* DC., and Wirth (2446) that in certain cells of the root of *Ceanothus americanus* there is a brownish substance whose colour is intensified by hydrochloric acid.

TAXONOMIC NOTES

Record and Hess (1886) have drawn attention to the occurrence of two distinct groups among the species of *Zizyphus*; one is characterized by diffuse apotracheal parenchyma, as in *Z. angolito* Standl. and *Z. sonorensis* S. Wats., the other by paratracheal parenchyma, as in *Z. jujuba* Mill., *Z. mistol* Gris., and *Z. spina-christi* Willd.

The species of *Rhamnus* also fall into two distinct groups; one group, corresponding to the sub-genus *Eurhamnus*, having a marked oblique or dendritic vessel pattern, the other, corresponding to the sub-genus *Frangula*, having vessels that are semi-ring-porous, but otherwise without pattern. Record and Hess consider that the species furnishing the Red or Pink Ivory of northern Natal, *Rhamnus zeyheri* Sond., is out of place in this genus.

ECONOMIC USES

The timbers of this family are of little importance. *Maesopsis berchemoides* A. Chev. in East Africa, however, is a very large tree furnishing a soft timber with some possibilities. Some species of *Zizyphus* are, or have been, used locally, e.g. the Jamaican Cogwood *Z. chloroxylon* (L.) Oliv. and *Z. jujuba* Mill. in India. Record and Hess (1886) note that *Colubrina*, *Karwinskia*, and *Rhamnidium* are the source of durable woods that are sometimes used locally, and *Sarcomphalus laurinus* Gris., though a small tree, is reputed to produce one of the best timbers in Jamaica. The charcoal of *Frangula alnus* Mill. was in great demand during the recent war for making powder for fuses.

The wood of *Krugiodendron ferreum* (Vahl.) Urban, with a specific gravity of up to 1.42 air dry, is reputed to be the densest known (1805).

The barks of various species of *Rhamnus* and *Ceanothus* are used in medicine because they possess laxative properties, whilst the fruits of *Rhamnus cathartica* Linn. are also used as a laxative in veterinary practice. The medicinal barks have been described anatomically and their chemical constituents discussed by Gathercoal (751), Greenish and Wallis (812), Hasler (917), Holm (1064), Maeder (1413), Taylor (2238), and Wirth (2446).

The bark of *Rhamnus purshiana* DC., the source of cascara sagrada, exhibits the following characters when sufficiently mature. Exposed outer surface purplish in colour when scraped. Cork consisting of 10-12 rows of thin-walled cells, sometimes filled with a brown deposit. Middle portion of the bark mainly parenchymatous, but containing elongated mucilage sacs (which become compressed and difficult to recognize in old material), stone cells, and rosette crystals. The inner portion of the bark, which arises only when the stems are sufficiently mature, consists of longitudinally elongated cells, and includes bundles of fibres sheathed by cells containing prismatic crystals. Large groups of stone cells also arise in the outer part of the inner bark between the somewhat sinuous, medullary rays which are 2-4 cells wide. The parenchymatous cells of the bark contain a yellow substance which is coloured violet by sodium hydroxide solution.

The bark of *Frangula alnus* Mill. (syn. *Rhamnus frangula* Linn.) is very similar to that of *R. purshiana* from which it may generally be distinguished by the absence of stone cells.

Hasler (917) experienced considerable difficulty in finding reliable characters for distinguishing between the barks from closely related species of *Rhamnus*, especially when variations in structure corresponding to different stages of maturity were taken into consideration. It was demonstrated, moreover, that the frequency of crystals varies according to the amount of calcium in the soil.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Alphitonia, Berchemia,* Ceanothus,* Colletia,* Colubrina, Condalia, Cormonema, Crumenaria, Cryptandra, Dallachya, Discaria,* Emmenosperra, Frangula,* Gouania,* Helinus, Hovenia, Karwinskia, Krugiodendron, Lamellisepalum, Lasiodiscus, Maesopsis, Marlothia, Microrhamnus, Noltea,* Paliurus,* Phyllica,* Pomaderris,* Reissekia, Reynosia, Rhamnella,

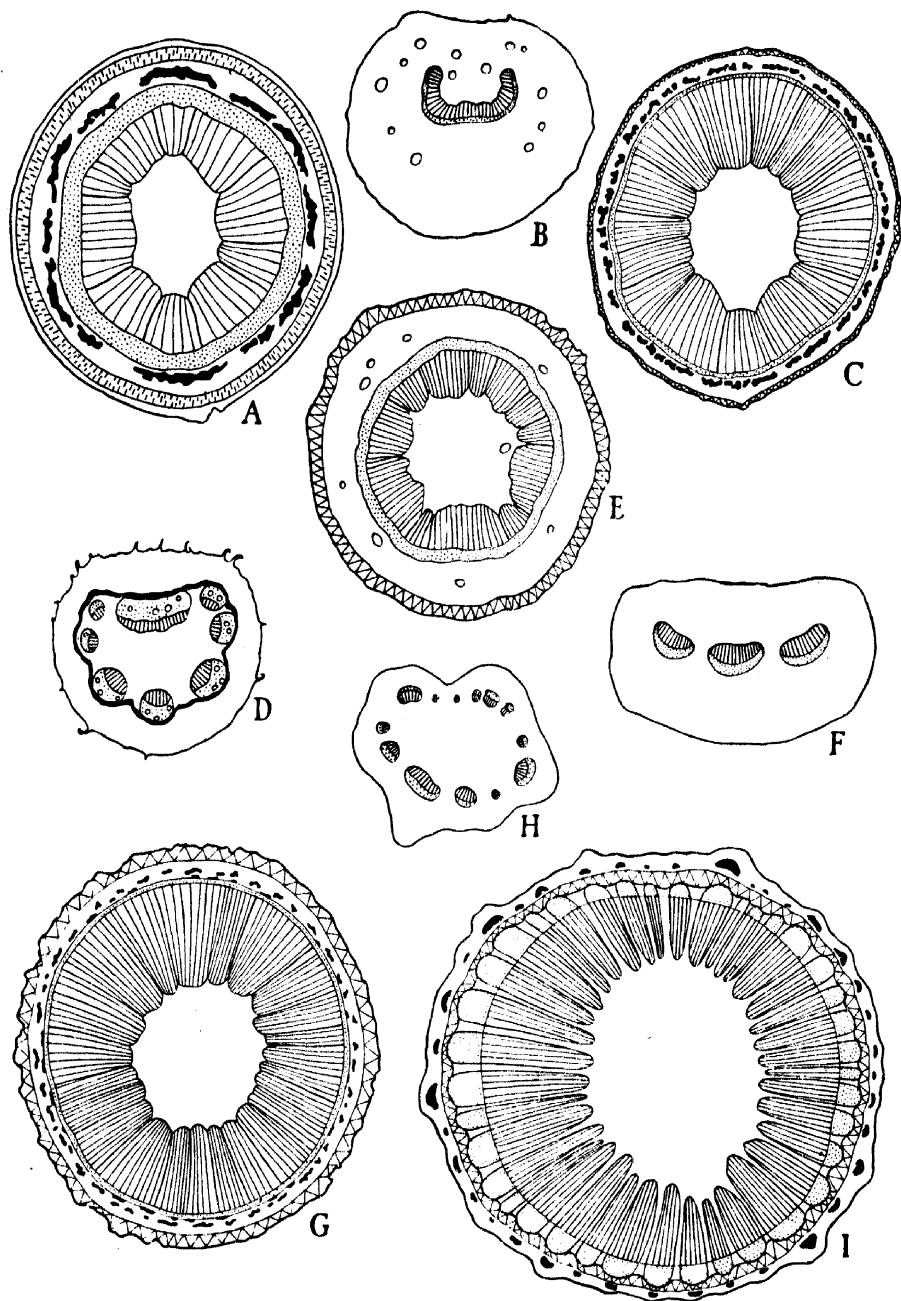


FIG. 93. RHAMNACEAE, A-C and E-F; AMPELIDACEAE, H-I; ACERACEAE, D and G
 A, *Discaria toumatou* Raoul. σ m \times 21. B, *Frangula alnus* Mill. (*Rhamnus frangula* Linn.). Petiole \times 31. C, *Pomaderris apetala* Labill. Stem \times 13. D, *Acer campestre* Linn. Petiole \times 32. E, *Frangula alnus* Mill. (*Rhamnus frangula* Linn.). Stem \times 17. F, *Paliurus spina-christi* Mill. Petiole \times 48. G, *Acer campestre* Linn. Stem \times 13. H, *Leea angulata* Korth. Petiole \times 8. I, *Vitis vinifera* Linn. Stem \times 15.

The small circles in B and E represent secretory (mucilage) cavities.

Rhamnidium, Rhamnus,* Sageretia, Sarcomphalus, Scutia, Spyridium, Talguenea, Trevoa, Trymalium, Ventilago, Zizyphus.*

* Slides in Kew collection.

(ii) FOR WOOD STRUCTURE

(Adolia), Alphonsea, Ampelozizyphus, Auerodendron, Berchemia, Ceanothus, Colletia, Colubrina, Condalia, Cormonena, Discaria, Doerpfeldia, Emmenosperra, (Gouania), Hovenia, (Karwinskia), Krugiodendron, Lasiodiscus, Maesopsis, Microrhamnus, Paliurus, (Phylla), Pomaderris, Reynosia, Rhamnella, Rhamnidium, Rhamnus, Sageretia, Sarcomphalus, Scutia, Ventilago, Zizyphus.

LITERATURE

(i) On General Anatomy

Bottomley 241, Chodat 398, Cooper 463, Gathercoal 751, Greenish and Wallis 812, Hasler 917, Heppeler 954, Holm 1064, Lamorlette 1316, Maeder 1413, Sabnis 1977, Taylor 2238, Watkins 2367, Weberbauer 2384, Wirth 2446.

(ii) On Wood Structure

Baker 104, Besson 186, Brown, F. B. H. 280, Brown, H. P. 289, Burgerstein 310, 312, Chowdhury 411, Cooper 461, Greguss 2522, Howard 1088, Janssonius 1154, Kanehira 1206, 1209, Messeri 1493, Normand 1613, Pearson and Brown 1679, Record 1783, 1805, 1843, 1851, 1856, Record and Hess 1886, Record and Mell 1894, Tang 2231, Williams 2430, Yamabayashi 2478.

100. AMPELIDACEAE

(VITACEAE)

(FIG. 93 on p. 412; FIG. 94 on p. 414; FIG. 95 on p. 416)

SUMMARY

(i) GENERAL

A tropical and sub-tropical family which includes many typical lianes, although some members, especially in the genus *Leea*, are erect and arboreal. The lianes are frequently much swollen at the nodes, and bear tendrils whose structure varies considerably in response to the nature of the substratum to which they become attached. For instance, they become coiled around stems and other cylindrical supports, but adhere to flat surfaces by means of cushion-like endings. Some species such as *Cissus currori* Hook. f. have a tuberous stem base serving mainly for the storage of water and from which erect branches arise. The morphology of the plants is often difficult to interpret. Some of the vines, especially those from the tropics, are provided with an extensive system of aerial roots. In correlation with the liane habit the young stem often exhibits a characteristic appearance in transverse section owing to the vessels being particularly wide in diameter, whilst the **xylem** is split up into lamellae by the broad primary and secondary medullary rays. This structure recalls that of the Aristolochiaceae. The family is also characterized by the presence of **raphides**, which are contained in sacs which sometimes appear under the lens as transparent dots or fine striae. Other forms of crystals include acicular, solitary and clustered types. The raphide sacs usually contain mucilage as well as the crystals, and in other instances **mucilage cells** occur from which

raphides are absent. Mucilage cells or large crystals sometimes appear as transparent dots in the same way as the raphide sacs.

The **hairs** are of the following types: simple unicellular; uniseriate; unicellular 2-armed; short stalked, glandular. Pearl glands and peltate scales also occur. The **stomata** are ranunculaceous. The **cork** arises superficially in some species, but in the cortex, pericycle, or even in the phloem in others. The **pericycle** contains isolated bundles of fibres or a composite and continuous ring of sclerenchyma. **Anomalous structure** has been recorded in *Cissus scariosa* Bl. (*Tetrastigma scariosum* Planch.) and related species.

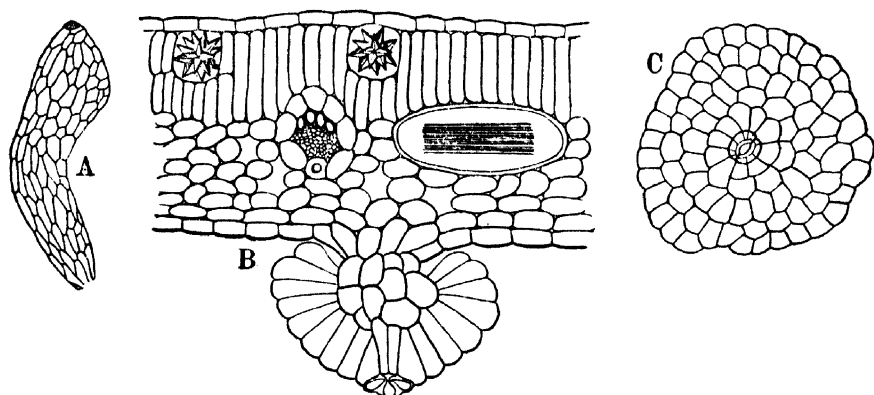


FIG. 94. AMPELIDACEAE

A, Pearl-gland of the vine. B-C, *Leea aequata* L.: B, Section through the leaf and through a gland; C, Surface-view of the gland.—A, after Penzig; B-C by Solereder.

(ii) WOOD

Vessels large in the climbers, small in *Leea*, radial multiples sometimes moderately common; perforation plates simple; intervascular pitting usually scalariform, sometimes opposite or alternate, pits to parenchyma simple and oblong, or bordered and round, members moderately short to very long. **Parenchyma** paratracheal, usually rather sparse, sometimes moderately abundant; forming the ground tissue in some species of *Cissus*; sometimes containing raphides. **Rays** broad and very high, up to 20 cells wide in some species, sometimes of 2 distinct sizes but more commonly with few or no uniseriate rays; cells varying from all procumbent to all square or upright; raphides present in many species. **Fibres** septate, very short to very long.

LEAF

Usually dorsiventral, with 1 or 2 layers of palisade tissue in *Vitis*; sometimes tending to be centric. **Hairs** of the following types. (i) Simple, uniseriate trichomes, with blunt or pointed ends, the component cells sometimes distinctly articulated. (ii) Simple, unicellular, sometimes very long and producing a felt resembling a spider's web. (iii) Unicellular, 2-armed, with or without stalks, notably in certain species of *Cissus*. (iv) Stalked glandular trichomes rare. Deciduous **pearl glands** common in *Cissus*, *Leea* (Fig. 94 B-C), and *Vitis*, but varying in frequency within a species, sometimes in relation to the vigour of the plant or the humidity of the atmosphere. These glands are

usually spherical structures each with a short stalk, the interior consisting of large, polygonal cells, surrounded by an epidermis perforated by a stoma, the latter usually but not invariably situated opposite the stalk of the gland. Cells of the glands rich in protein, oil, and sugar. Somewhat similar glands, composed of comparatively small, isodiametric cells and each surrounded by a palisade epidermis, and opening to the exterior by a solitary apical stoma, described in detail by Solereder in *Leea aequata* Linn. Walter (2354) has also investigated the structure and physiology of pearl glands in this family. **Leaf teeth** secreting mucilage in the bud of *Vitis vinifera* Linn. **Stomata** ranunculaceous in the few species examined. Stomatal distribution very imperfectly known. **Petiole** not examined in many species, but, in transverse sections, exhibiting a ring of isolated bundles, accompanied by two, or less frequently more, cortical bundles on either side of the groove in the adaxial surface of the petiole in certain species of *Leea* (Fig. 93 H) and *Vitis*. **Secretory cells** with amorphous contents (probably mucilaginous and tanniniferous) widely distributed in the parenchymatous tissues, notable in the petiole of *Leea angulata* Korth. and *Vitis vinifera* Linn. and probably in other genera and species. Large mucilage cells, also appearing as dots, recorded in species of *Cissus*, *Parthenocissus*, and *Vitis*. **Raphide sacs** (see also 'Summary'), of variable lengths and often containing mucilage, occur throughout the family, the individual raphides stated to be pointed at one end but bidentate at the other in *Cissus* and *Vitis*. Solitary and clustered **crystals** also common; druses in *Leea* especially large and sometimes appearing as dots.

Dune forms of *Pseodera quinquefolia* (L.) Greene and *Vitis vulpina* Linn. have been recorded by Starr (2188) as having taller palisade cells, and epidermal cells which are larger in surface area but shorter than those in mesophytic specimens of the same species. In *Vitis vulpina* hairs were observed by the same author above the veins on both surfaces in dune specimens, but were confined to the same position on the upper surface in mesophytic forms.

AXIS

YOUNG STEM (Fig. 93 I)

Often very characteristic, as seen in transverse section, owing to the particularly wide diameter of the vessels and the appearance of the lamellae of **xylem** and phloem separated by the broad, primary, and secondary medullary rays. **Cork** in *Parthenocissus quinquefolia* Planch. arising immediately below the epidermis. In the same species successive annual growths, produced from the same phellogen, remain separated from one another by a layer of sclerotic cork. Cork stated to arise in a similar manner in *Cissus*, *Leea*, and certain species of *Vitis*; originating in the pericycle and consisting mainly of thin-walled cells, with solitary sclerotic cells amongst them in *Vitis vinifera* Linn. (Fig. 93 I) and other closely related species of *Vitis*. Primary **cortex** said to contain cells with perforations in *Cissus antarctica* Vent. **Pericycle** containing isolated strands of fibres in *Leea angulata* Korth. as well as in *Vitis vinifera* and closely related species, but exhibiting transitions between this arrangement and a composite continuous ring of sclerenchyma in other species. Pericyclic fibres with wide lumina and thin walls in *Vitis vinifera* and closely related species, but short-lived owing to the development of deep-seated

cork. Secondary **phloem** stratified into sclerosed and soft portions in the *Euvitis* section of *Vitis*, but with the fibres arranged in more or less radial rows beside the medullary rays and exhibiting a scattered arrangement in the

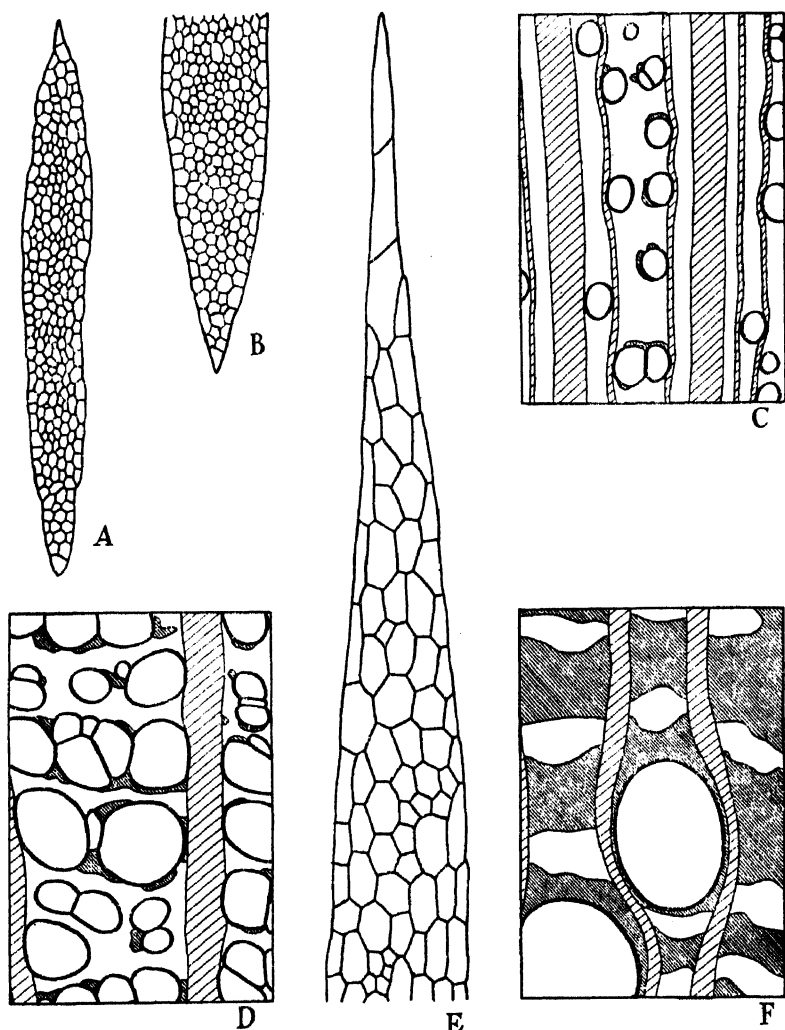


FIG. 95. AMPELIDACEAE

A, *Parthenocissus vitacea* Hitchc. B, *Vitis arizonica* Engelm. C, *Leea guineense* Don. D, *Vitis labrusca* Linn. E, *Leea philippinensis* Merr. F, *Cissus sicyoides* Linn.

inner part of each phloem strand in the *Muscadinia* section of the same genus. Phloem and **xylem** forming crowded but individually distinct vascular bundles separated by broad primary medullary rays in *Vitis vinifera* (Fig. 93 1) and other species. Vessels wide in climbers; perforations simple. **Pith** composed of cells with walls of variable thickness in different species; homogeneous or heterogeneous. Cluster and solitary **crystals** and raphides

common in the parenchymatous tissues. Acicular crystals, smaller than typical raphides and not embedded in mucilage, also recorded in the cortex and phloem of various members of the family, notably in species of *Ampelopsis* and *Cissus*. **Secretory cells** with amorphous contents (probably mucilaginous and tanniniferous) widely distributed in the parenchymatous tissues of the stem in *Leea angulata* Korth, *Vitis vinifera*, and probably in other genera and species as well.

WOOD (Fig. 95)

Vessels small in *Leea* (less than $100\ \mu$ mean tangential diameter), large (more than $200\ \mu$) in the climbers *Cissus*, *Parthenocissus*, *Psedera*, *Tetrastigma*, and *Vitis*, largest vessels up to $350\ \mu$ in tangential diameter; of 2 types in *Parthenocissus* and some species of *Vitis*, the larger solitary and often over $300\ \mu$ in diameter, the smaller seldom exceeding $100\ \mu$ in diameter and either commonly in radial multiples (*Vitis*) or grouped round the larger vessels (*Parthenocissus*); radial multiples common also in *Psedera*; very variable in number even in the same genus, from 2 to 22 per mm.; ring-porous in some species of *Vitis* (1851). Perforations simple. Intervascular pitting usually scalariform, locally opposite in *Psedera* and alternate in *Cissus sicyoides* Linn., *Parthenocissus*, and *Tetrastigma*; pits to parenchyma round and bordered in woods with alternate intervacular pitting, large, oblong, and often simple in the others, usually with the long axes horizontal. A few tyloses present in most species of *Cissus*, *Parthenocissus*, and *Vitis*, sometimes locally abundant. Mean member length very variable, e.g. *Parthenocissus* $0.3\ \text{mm.}$, *Vitis* $0.7\ \text{mm.}$, and *Leea* $1.7\ \text{mm.}$ **Parenchyma** paratracheal, varying from a few cells round the vessels (Fig. 95 c and d) to a well-defined vasicentric sheath, but never abundant; according to Kanehira (1206) sparse and scattered among the fibres in *Leea sambucina* Willd. In certain soft-stemmed species of *Cissus*, e.g. *C. sicyoides* L., according to Solereder (2158) 'the groundwork of the wood consists of unlignified parenchymatous tissue with thin walls, in which the vessels are embedded in groups, each group surrounded by a sheath consisting of a little lignified wood-parenchyma and wood-prosenchyma' (Fig. 95 F). A similar type of structure occurs in *Parthenocissus*. Hess (959) reports the occurrence of raphides in this tissue in *Cissus* and there may also be chambered solitary crystals on the margins of the sheaths where they join the fibres. Strands usually of 4 cells, sometimes up to 8 cells. Storied in *Parthenocissus* and *Tetrastigma*. **Rays** broad (more than $100\ \mu$) and usually very high; commonly of indeterminate height, but exhibiting various stages of dissection into smaller units in some species; the larger rays 4–6 cells wide in *Cissus* and *Leea* p.p., up to 15–20 cells wide in some species of *Psedera* and *Vitis*; of 2 distinct sizes (uniseriate or broad) in *Leea*, *Vitis arizonica* Engelm., and *V. californica* Benth. (8); with a fairly complete gradation of sizes in *Cissus sicyoides* L. and *Parthenocissus*; normally without uniseriate rays in most species of *Vitis* (8) and with few or none in *Cissus*, some species of *Leea*, *Psedera*, and *Tetrastigma*; uniseriates varying from high upright cells in *Leea* p.p. to procumbent in *Parthenocissus*; Adkinson (8) notes that, as a result of injury, uniseriate rays may occur in woods from which they are normally absent. Between 2 and 6 rays per mm. in woods with large rays only, up to 12 per mm. in woods with uniseriate rays; cells of the multiseriate rays all

upright or square in *Leea* (Fig. 95 E) and *Sundaica*, almost all procumbent in *Parthenocissus*, *Psedera*, and *Vitis* p.p., in other species a mixture of square to procumbent cells without any distinct marginal rows; cells very variable in tangential width in different species, relatively small where the cells are all procumbent (Fig. 95 A and B), e.g. *Psedera*, and large where true procumbent cells are rare (Fig. 95 E); sheath cells present in some species; cells typically filled with dark contents and containing occasional single crystals in some species. Raphides occur in the rays of *Leea*, *Tetrastigma*, and *Vitis*. The small rays storied in *Parthenocissus*. **Fibres** septate and frequently containing dark deposits; pits simple and usually more numerous on the radial than on the tangential walls, with small borders in *Leea tetramera* B. L. Burtt. With moderately thin walls in most species. In *Cissus sicyoides* and *Parthenocissus* the fibres do not form the ground tissue but occur in narrow bands or patches separated by more abundant thin-walled parenchyma (Fig. 95 F); they are non-septate, very thick-walled, much elongated (5 times the length of the vessel members or more) and very long (nearly 3 mm. in *Cissus*). Storied in *Tetrastigma lauterbachianum* Gilg. Mean length very variable, e.g. *Parthenocissus* 0.6 mm., *Vitis* 1.4 mm., and *Leea* 2.4 mm. Vasicentric **tracheids** reported by Record and Hess (1886); with scalariform thickening and sometimes with delicate spiral thickening. **Intercellular canals** of the vertical traumatic type observed in *Cissus sicyoides* L.

Root

The particulars recorded by Turner (2300) about the aerial roots of *Vitis rotundifolia* Michx. include the following. **Epidermis** short-lived; apparently devoid of stomata. Primary **cortex** 15–25 cells wide; outer part collenchymatous, but provided with well-developed intercellular spaces towards the interior. Raphide sacs present in the cortex, but crystals becoming dissolved during development of the root, and the cells containing them disorganized. **Endodermis** consisting of cells with thickened walls and serving mainly for storage; casparian thickenings only rarely observed. Primary **vascular system** hexarch to octarch. Secondary thickening proceeds normally. Vessels in the secondary xylem up to 200 μ in diameter; tyloses fairly common. **Pith** composed of cells with slightly thickened walls; still persisting in 7-year-old roots.

ANOMALOUS STRUCTURE

Anomalous secondary thickening has been described in *Cissus scariosa* Bl. (*Tetrastigma scariosum* Planch.) by Schenck whose description was followed by Solereder (2158) and is repeated here. The strap-shaped stem grows in thickness in the normal way until it is 1 cm. thick. At this stage the individual segments of xylem and phloem are separated by broad parenchymatous rays. In each segment of xylem and phloem on the narrow side of the stem a strip of cambial tissue arises in the phloem parenchyma, immediately on the inside of the first-formed strand of phloem. The newly formed strip of cambium then gives rise to fresh xylem and phloem. Certain other species of *Tetrastigma* are said to exhibit a similar anomaly.

PHYLOGENETIC AND TAXONOMIC NOTES

Adkinson (8), after making a comparative anatomical study of a selection of the Vitaceae, concluded that the erect members of the family such as *Leea* retain more primitive characters than the climbers. In the primitive erect types the broad medullary rays are accompanied by linear rays which have been lost in most of the climbing species, although still retained in *Vitis californica* Benth. In some other members of the Vitoideae vestiges of linear rays persist in the seedling and 'conservative' parts of the plant. Adkinson also concluded that '*Ampelopsis*' and *Cissus*, where the xylem is more reduced and dissected than in *Vitis*, are the more primitive genera. The vine is regarded as an approach to the herbaceous (advanced) type of stem.

Hess (959) suggests that the wood of *Leea* bears some relation to Dilleniaceae.

ECONOMIC USES

The most important economic plant in the family is *Vitis vinifera* Linn. the grape vine, from the fruits of which wines are prepared, while those of certain varieties, when dried, are most familiar as raisins, currants, &c. The Virginia Creeper of gardens is *Parthenocissus tricuspidata* Planch.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Ampelopsis, *Cissus*, *Leea*,* *Parthenocissus*, *Psedera*, *Tetrastigma*, *Vitis*.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Cissus, *Leea*, *Parthenocissus*, *Psedera*, *Tetrastigma*, *Vitis*.

LITERATURE

(i) *On General Anatomy*

Adkinson 8, Bowman 250, Esau 2518, Gilg 767, La Rivière 1320, Rehder 1903, Starr 2188, Turner 2300, Walter 2354.

(ii) *On Wood Structure*

Adkinson 8, Dadswell and Record 533, Desch 574, Greguss 2522, Greiss 817, Hess 959, Howard 1088, Janssonius 1154, Kanehira 1206, Pfeiffer, H. 1712, Record 1818, 1843, 1851, Record and Hess 1886.

✓101. SAPINDACEAE

(FIG. 96 on p. 424; FIG. 97 on p. 426; FIG. 100 on p. 438)

SUMMARY

(i) GENERAL

Trees, shrubs, and lianes mainly from tropical but also from temperate regions. The lianes frequently exhibit anatomical peculiarities in the stems, and also possess tendrils. Thorns, which represent reduced axillary branches, occur in *Stocksia*. Of the erect members of the family some are branchless with a terminal collection of leaves and thus resemble palms or tree ferns. Species of *Pseudima*, *Pseudopteris*, *Talisia*, *Toulucia*, *Tripterodendron* possess this unusual habit form. The hairs may be either (i) simple, unicellular with

a tendency to be 2-armed; (ii) tufted; (iii) small peltate scales. Small glandular hairs are also frequent, particularly in young leaves. The colour of the **leaf** in herbarium specimens is somewhat distinctive in certain genera (see 'Leaf'). The **epidermis** of the leaf often includes mucilaginous cells which appear as transparent dots. Small translucent areas are also caused by the presence of **secretory cells**. The lower surface of the leaf is often papillose. The **stomata**, usually confined to the lower surface, are ranunculaceous except in *Conchopetalum* and *Harpullia*. **Hypoderm** is often present. The **mesophyll** is usually dorsiventral, but wholly or partly centric in certain genera; it often includes sclerenchymatous fibres. **Crystals** are mostly solitary or clustered, whilst crystal-sand has been recorded in *Exothea* and styloids in *Diatenopteryx*. The **cork** in the young stem is superficial in origin in most instances. The **pericycle** contains a composite and continuous ring of sclerenchyma except in *Valenzuelia* and *Xanthoceras*. Several types of **anomalous thickening** have been described in a number of genera. **Saponin** is commonly present in the tissues.

(ii) WOOD

Vessels typically small and numerous, with many multiples of 2-3 cells, but without any definite pattern; perforations simple, intervascular pitting alternate and small to minute; pits to parenchyma similar. Very occasionally ring-porous or with spiral thickening; members of medium length to very short. **Parenchyma** most commonly paratracheal only and sparse, sometimes vasicentric, with isolated crystalliferous strands or diffuse parenchyma scattered among the fibres, or in confluent bands; terminal parenchyma sometimes prominent. **Rays** typically exclusively uniseriate or nearly so, low, numerous and homogeneous; 2-3 cells wide in a few genera and occasionally heterogeneous. **Fibres** with simple pits and typically septate, though septa may be few or lacking where the fibres are very thick walled; of medium length to very short.

LEAF

Usually dorsiventral; wholly or partly centric in certain species of *Cardiospermum*, *Diplopeltis*, *Dodonaea*, *Elattostachys*, *Erythrophysa*, *Heterodendron*, *Koelreuteria*, *Lecaniodiscus*, *Paullinia*, *Stocksia*, *Xanthoceras*. **Hairs**. (i) Unicellular, or tending to be uniseriate, often with swollen, sometimes striate bases sunk below the epidermis in species of *Cardiospermum* (pointed), *Chytranthus*, *Matayba*, *Pancovia*, *Xerospermum*. (ii) Unicellular but tending to be 2-armed in *Alectryon*, *Matayba*, *Nephelium*, *Pometia*, *Stadmannia*. (iii) Multicellular, tufted or stellate hairs, sometimes accompanied by simple ones in *Arfeuillea*, *Cossignia*, *Euphoria*, *Harpullia*, *Nephelium*, *Xanthoceras*. (iv) Glandular hairs, each with a short uniseriate stalk and an oval head of a few cells, very common, possibly present throughout the family on young leaves. (v) Small multicellular peltate scales recorded in species of *Arytera*, *Cupaniopsis*, *Dictyoneura*, *Dodonaea*, *Filicium*, *Ganophyllum*, *Lecaniodiscus*, *Lepiderema*, *Lychnodiscus*, *Smelophyllum*, *Stadmannia*. Glandular hairs sometimes specially large in *Crossonephelis*, *Melanodiscus*, and *Talisia*; complex in structure and occasionally containing solitary and clustered crystals in the head in *Llagunoa* and *Loxodiscus*. Glandular hairs not observed in all or

certain species of *Castanospora*, *Chytranthus*, *Conchopetalum*, *Cupania*, *Dodonaea*, *Eriandrostachys*, *Gleniea*, *Harpullia*, *Macphersonia*, *Matayba*, *Melicocca*, *Molinaea*, *Otophora*, *Pancovia*, *Phialodiscus*, *Porocystis*, the *Schleichereae*, *Storthocalyx*, *Tina*, *Toechema*, *Toulícia*, *Trigonachras*, *Tristira*, *Tristiropsis*, *Valenzuelia*, *Xanthoceras*. Dried leaf lead-grey or yellowish-green in external appearance in the *Aphanieae*, *Cupanieae*, and *Lepisantheae* owing to special contents of the epidermis; lower side chocolate-brown owing to tanniniferous contents of the mesophyll in *Guioa*, *Nephelium*, and *Otophora*; blackish-brown in *Elattostachys*, blackish-green in *Harpullia*; young dried leaves reddish in *Nephelium*, *Otophora*, *Pometia*, *Schleichera*, *Talisia*. Leaves and branches sometimes covered with a resinous secretion from the external glands in species of *Dodonaea*, *Filicium*, *Ganophyllum*, and *Llagunoa*. **Epidermis** composed of cells with sinuous anticlinal walls and pits in the bays of the undulations in all or certain species of *Alectryon*, *Aporrhiza*, *Arytera*, *Atalaya*, *Blighia*, *Chytranthus*, *Cupaniopsis*, *Doratoxylon*, *Eriocoelum*, *Euphoria*, *Exothea*, *Guioa*, *Haplocoelum*, *Harpullia*, *Laccodiscus*, *Lecaniodiscus*, *Lepiderema*, *Lepidopetalum*, *Lychnodiscus*, *Matayba*, *Melanodiscus*, *Mischocarpus*, *Pancovia*, *Phialodiscus*, *Sarcopteryx*, *Sarcotoechia*, *Storthocalyx*, *Synima*, *Toechema*, *Trigonachras*, *Xerospermum*. Some of the epidermal cells sclerosed in *Matayba purgans* (Poepp. et Engl.) Radlk. Epidermal cells particularly tall in *Deinbollia*, *Otophora*, and *Sarcopteryx*; provided with delicate, vertical, secondary walls in species of *Alectryon*, *Arytera*, *Cupaniopsis*, *Euphoria*, *Heterodendron*, *Macphersonia*, *Tina*, *Xerospermum*; with secondary walls parallel to the leaf surface in *Cupaniopsis* and *Gongrodiscus*. Mucilaginous cells frequent in the epidermis, sometimes appearing as transparent dots; occurring throughout some of the genera, but limited to certain, often closely related, species in others. Papillae often present on the lower surface, sometimes forming a network owing to their being united to one another by cuticular ridges. (For further details of mucilaginous epidermal cells and papillae see Solereder.) **Stomata** reported to be unusually small in *Cupania*, *Nephelium*, *Sapindus*, *Talisia*, and other related genera, but much larger in *Aphania* and *Otophora*, usually confined to the lower surface, but present on both sides in certain species of *Dodonaea*, *Lepiderema*, *Pappea*, *Paullinia*, *Serjania*; known to be rubiaceous in species of *Conchopetalum* and *Harpullia*, elsewhere ranunculaceous. Stomata particularly numerous but small in *Arytera*, *Dilodendron*, *Elattostachys*, *Guioa*, *Lepidopetalum*, *Mischocarpus*, *Molinaea*, the *Nephelieae*, *Paranephelium*, *Porocystis*, *Sapindus*, *Sarcotoechia*, *Schleichera*, *Talisia*, *Toechema*, *Toulícia*, *Tristira*; much larger but less numerous in *Aphania* and *Otophora*. Parenchymatous **hypoderm** present in certain species of *Alectryon*, *Arytera*, *Atalaya*, *Conchopetalum*, *Cupania*, *Harpullia*, *Matayba*, *Molinaea*, *Storthocalyx*, *Talisia*; hypodermal cells fibrous in *Euphoria gardneria* Thw.; filled with a soft, homogeneous or lamellated substance of unknown chemical nature in *Cossinia*. **Mesophyll** containing sclerenchymatous fibres or sclerosed cells in certain species of *Cupaniopsis*, *Haplocoelum*, *Harpullia*, *Matayba*, *Paullinia*, *Serjania*, *Xerospermum*; similar cells also recorded by Le Renard (1363) in the rachis of *Arfeuillea*, &c. Intercellular spaces in the spongy mesophyll particularly large in *Eriandrostachys*, *Ganophyllum*, *Harpullia*, *Otonephelium*, *Otophora*, *Paranephelium*, *Plagioscyphus*, *Pseudonephelium*; almost or completely absent from species of

Alectryon, *Arytera*, *Atalaya*, *Averrhoidium*, *Cupaniopsis*, *Elattostachys*, *Melicocca*, *Pappea*, *Podonaphelium*, *Talisia*, *Tina*, *Toulicia*. Palisade cells transversely septate in species of *Alectryon*, *Eriandrostachys*, *Macphersonia*, *Magonia*, *Nephelium*, *Otonaphelium*, *Pometia*, *Xanthoceras*; hour-glass shaped in *Lepidopetalum*; top shaped in *Harpullia*; scarcely longer than broad in *Rhysotoechia* and *Toechia*; provided with small transverse folds in *Conchopetalum*. **Veins** vertically transcurrent in *Alectryon*, *Athyana*, *Bridgesia*, *Cardiospermum* (larger veins only), *Diatenopteryx*, *Euphoria*, *Hornea*, *Litchi*, *Mischocarpus*, *Nephelium*, *Pappea*, *Paranaphelium*, *Plagioscyphus*, *Porocystis*, *Stadmannia*, *Synima*, *Thouinia*, *Thouinidium*, *Toulicia*, *Xerospermum*; surrounded by a ring of sclerenchyma in *Tristiropsis*. Smaller veins often embedded in the mesophyll. The presence or absence of sclerenchyma around the veins is said to be of value in the identification of species. **Petiole** exhibiting, in transverse sections through the distal end, a continuous, approximately circular strand or a circular group of separate strands. In the material available for examination a continuous vascular strand was observed in species of *Koelreuteria* (Fig. 100 B), *Nephelium*, and *Xanthoceras* (Fig. 100 I), and separate bundles in species of *Dodonaea*, *Paullinia*, *Xanthoceras*. Additional vascular strands sometimes present in the cortical region, e.g. in *Paullinia cupana* Kunth (Fig. 100 C); medullary bundles also observed, e.g. in *Nephelium longana* Lam. and *Paullinia cupana*. Four isolated bundles recorded in the relatively herbaceous species *Cardiospermum halicacabum* Linn. Main vascular strand of the petiole surrounded by a circle of sclerenchymatous fibres in all of the species examined except *Dodonaea viscosa* (L.) Jacq. Le Renard (1363) observed 3 separate vascular strands in the base of the leaf of various species of *Arfeuillea*, *Cossignia*, *Harpullia*, &c., but transverse sections at a higher level in the rachis revealed a triangular, and, near the distal end of the rachis, a circular vascular strand formed by the fusion of the 3 basal bundles. **Crystals** mostly solitary or clustered; crystal-sand recorded in *Exothea*. Crystals particularly frequent in the epidermis in species of *Chytranthus*, *Conchopetalum*, *Filicium*, *Ganophyllum*, *Pancovia*, *Paullinia*, *Pometia*, *Xerospermum*. Clustered and/or solitary crystals generally present in the soft tissues of the petiole; none observed in *Koelreuteria paniculata* Laxm. **Secretory cells** (see also 'Epidermis', 'Young Stem', and 'Petiole'), either tubular and sometimes forming uniseriate rows of variable lengths, or rounded and irregular in shape, commonly, but not universally, present in the leaf, sometimes appearing as transparent dots. The contents, believed to be a substance resembling saponin, are stated to resemble latex in living specimens, but appear to be clear or turbid and vary in colour from yellowish-brown to brownish-black in herbarium material. Contents of the secretory cells in *Erythrophysa* and *Stocksia* give a tannin reaction; stated to consist of chlorophyll in *Paranaphelium*. Further details quoted by Solereder.

AXIS

YOUNG STEM (Fig. 96 A-F and 100 D and F)

Surface with ribs (collenchymatous) in some species, e.g. *Cardiospermum halicacabum* Linn. **Cork** nearly always arising in the sub-epidermis or outer part of the primary cortex; originating within the pericyclic sclerenchyma only in *Distichostemon* and *Dodonaea*. The phellogen in these last 2 genera produces

sclerenchyma as well as cork, a second sclerenchymatous ring being formed in the phelloderm. By repetition of this process the branch eventually becomes covered by a 2- to 4-fold layer of cork and sclerenchyma. Primary **cortex** collenchymatous, especially at the angles of the stem, particularly in species climbing by tendrils; containing groups of stone cells in certain species of *Atalaya*, *Melicocca*, *Sapindus*, and *Talisia*, or a ring of stone cells in *Toulicia guianensis* Aubl. Le Renard (1363) observed collenchyma to be absent from the cortex in species of *Arfeuillea*, *Cossignia madagascariensis* Bail., and *Harpullia pendula* F. v. M., whereas it occurred in all other species of *Harpullia* examined as well as in *Koelreuteria paniculata* Laxm. **Pericycle** generally containing a composite ring of sclerenchyma when sufficiently mature, but, when younger, provided with an interrupted or almost continuous circle of fibres in certain species. The occurrence of stone cells has not been demonstrated in a few instances, notably in species of *Cupania*, *Dodonaea*, *Valenzuela*, and *Xanthoceras*, but this may have been because the material was not sufficiently mature. Primary **phloem** containing fibres with infrequent transverse partitions in species of *Cardiospermum* and *Serjania*; phloem fibres and/or sclerosed cells also observed by Le Renard (1363) in *Arfeuillea*, *Cossignia*, *Harpullia*, and *Koelreuteria*. Secondary phloem in other genera containing few or no fibres, but stone cells sometimes present in this position. **Xylem** usually in the form of a continuous cylinder, traversed by rays 1-2 cells wide. Vessels commonly isolated, but sometimes in groups; perforations simple. Concentric zones of xylem parenchyma observed by Le Renard (1363) in young stems of *Cossignia madagascariensis* Bail., but not in species of *Arfeuillea*, *Harpullia*, &c. **Pith** sometimes including stone cells; consisting almost wholly of these elements in species of *Molinaea*; composed of thin-walled cells in *Cardiospermum halicacabum* Linn. Le Renard (1363) observed (i) groups of rounded sclerosed cells with pitted walls in the pith of *Arfeuillea* and *Harpullia thanatophora* Bl.; (ii) vertical rows of elongated sclerosed cells in *Harpullia cupanioides* Roxb.; (iii) irregularly ramifying strands of more rounded cells in other genera and species. Rudimentary vascular bundles, or bundles consisting wholly of fibres, sometimes met with in the pith of *Guioa*, *Mischocarpus*, *Toulicia*, and *Tristiropsis*. **Secretory cells**, similar to but less easily visible than those of the leaf, present in the primary cortex and secondary phloem as well as in the pith; varying in size and distribution in different genera and species; sometimes arranged in longitudinal series. Both solitary and/or clustered **crystals** common in the parenchymatous tissues; details concerning their occurrence and distribution probably of value for the identification of species. Besides crystals elsewhere in the ground tissue, Le Renard (1363) observed them in a layer of endodermal cells in species of *Arfeuillea*, *Cossignia*, *Harpullia*, and *Koelreuteria*.

ANOMALOUS STRUCTURE

Several types of anomalous structure have been recorded in lianes belonging to this family. (i) **A compound xylem-mass** (Fig. 96 A) consisting of a central ring of bundles, surrounded by but separated from several peripheral rings of bundles by a small amount of cortical parenchyma. The bundles in the central and peripheral rings are each provided with a separate pith, and each grows in thickness by its own cambium. The central and peripheral

bundles are interconnected at the nodes. This type of structure, which produces ribs on the stems, is confined to 91 out of 172 species of *Serjania* and 16 out of 122 of *Paullinia*; it is unknown in other families except possibly in the Leguminosae. (ii) The **divided xylem-mass** (Fig. 96 B) is similar to the structure just described, but the central vascular ring is absent, the main pith being surrounded by 5-7 rings of xylem and phloem, which remain open

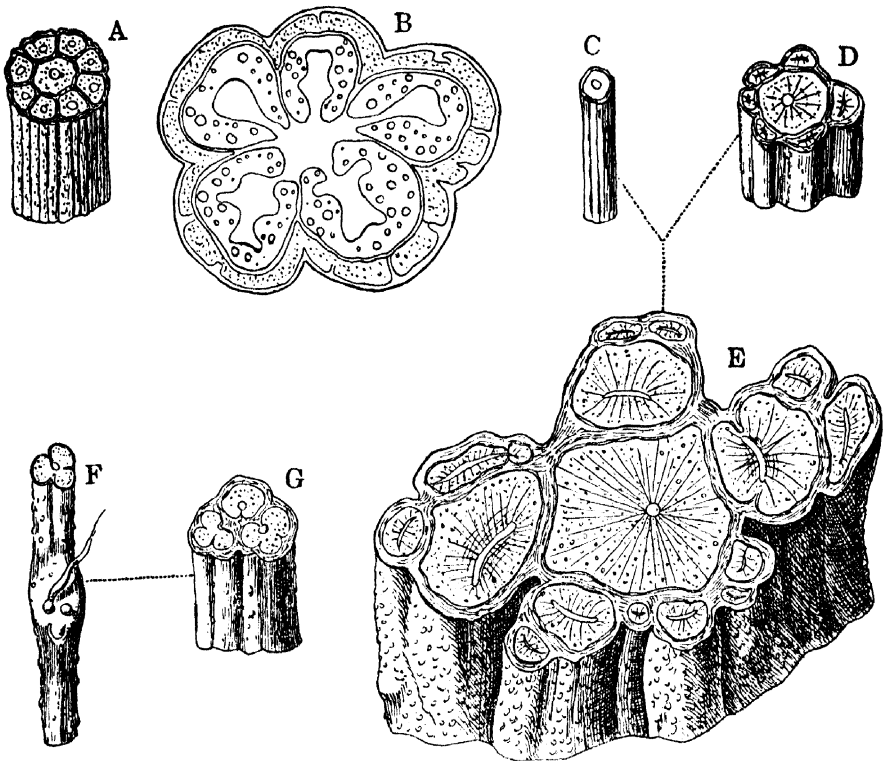


FIG. 96. SAPINDACEAE

A, Compound xylem-mass of *Serjania fuscifolia* Radlk. B, Divided xylem-mass of *Serjania corrugata* Radlk. C-E, Corded xylem-mass of *Thoinoua ventricosa* Radlk. and other species at three successive stages representing different ages. F-G, Cleft xylem-mass of *Urvillea laevis* Radlk. at two stages in the growth.—After Radlkofer.

on the inside for a considerable time, so that their individual piths are connected with the main one at the centre. This type is known only in *Serjania corrugata* Radlk. and closely related species. (iii) The **corded xylem mass** (Fig. 96 C-E). In this type growth proceeds normally for 5 or 6 years, after which accessory cambia arise in the cortical parenchyma externally to the original vascular ring and produce subsidiary rings of xylem and phloem each enclosing a separate pith. The accessory vascular rings are thus connected with one another but not with the original vascular ring. This type is stated to occur in all species of *Thoinoua*, in a few of *Paullinia*, and sometimes as a secondary complication in species exhibiting compound or divided xylem masses as described above. (iv) The **cleft xylem mass** (Fig. 96 F-G). Here

also the structure is at first normal, but superficially grooved, owing to certain portions of the cortex being rather strongly depressed. The axis subsequently becomes split into 3 or more portions corresponding to the grooves, owing to the appearance of cambial tissue at these points. The separate portions of the stem then grow in thickness through the activity of a cambium, which surrounds each of them on all sides. Lastly a lobed xylem-mass originates by increased development of the wood at 5 or more places at the circumference of the stem; 5 or more ribs are formed, which project externally, and are separated from one another by narrow grooves. This structure occurs in some species of *Serjania* and *Urvillea*.

The exposed surface of the sapwood beneath the bark of the following trees exhibits a 'corduroy' appearance owing to the presence of longitudinal corrugations: *Alectryon connatus* Radlk., *Arytera lautereriana* Radlk., *Diploglottis cunninghami* Benth., *Guioa semiglaucula* Radlk., *Sarcopteryx stipitata* Radlk. According to Francis (708) transverse sections of young stems of *Arytera lautereriana* exhibit 5 indentations alternating with an equal number of ribs on the surface of the woody cylinder, where they correspond to the outline of the pith. Smaller indentations occur in the region of the node where they are related to the median and lateral leaf traces. Transverse sections of a stem 9 cm. in diameter showed some of the depressions to correspond to small areas of cells containing a brown tanniferous substance, associated with thick-walled pitted parenchymatous elements not found in the normal wood. These areas were thought to be caused by injury, possibly by insects. The prominent indentations of mature trees were found to be connected with pairs of large aggregate rays terminating at the surface of the sapwood where the indentations occur. The indentations in *Sarcopteryx stipitata* Radlk. are likewise associated with similar pairs of large aggregate rays.

WOOD (Fig. 97)

Vessels typically small (mean tangential diameter less than $100\ \mu$), very small (less than $50\ \mu$) in *Cupania* p.p., *Diplokeleba*, *Diatenopteryx*, *Doratoxylon*, *Exothea*, *Glossolepis*, *Hippobromus*, *Pappea*, *Stadmannia*, *Thouinia*, and *Thouinidium*, medium-sized (100 – $200\ \mu$) in *Blighia*, *Castanospora*, *Chytranthus*, *Cubilia*, *Cupaniopsis*, *Lecaniodiscus*, *Lepisanthes*, *Paranephelium*, *Paullinia*, *Pometia*, *Sapindus*, *Schleichera*, *Schmidelia*, *Talisia*, *Tristira*, *Tristropsis*, and *Ungnadia*; typically with numerous multiples of 2 or 3, the multiples tending to be 8- rather than θ -shaped, with multiples of 4 or more moderately common in *Dodonaea*, *Hippobromus*, *Laccodiscus*, *Nephelium*, and *Placodiscus*, with fewer multiples and most of the vessels solitary in *Blighia*, *Cubilia*, *Cupaniopsis*, *Deinbollia*, *Eriocoelum*, and *Pometia*, with a tendency to a loose oblique pattern (Fig. 97 H) in some specimens of *Athyana*, *Blighia*, *Cupania* (1886), *Hypelate* (1886), and *Lecaniodiscus*; with a tendency to form longer multiples locally in many species, probably in response to injury; Heimsch (938) notes clusters in species of *Dodonaea*, *Koelreuteria*; *Pappea*, *Podonephelium*, *Sapindus*, and *Tina*; of 2 distinct sizes in *Paullinia*, the larger solitary, the smaller in long radial multiples; varying in number from about 2 to 50 per mm., mostly 2–5 and not more than 10 per mm. in woods with medium-sized vessels, 10–50 per mm. in woods with very small vessels, sometimes relatively few and widely spaced in woods with moderately small

vessels, e.g. *Cupania*, *Erioglossum*, *Glossolepis*, *Placodiscus*, and *Stadmannia*; ring-porous or semi-ring-porous in some species of *Hypelate* (1864), *Koelreuteria*, and *Sapindus*; spiral thickening not observed but reported (1206) in species of *Allophylus*, *Blighia*, *Cupaniopsis*, *Exothea*, *Guioa*, *Koelreuteria*,

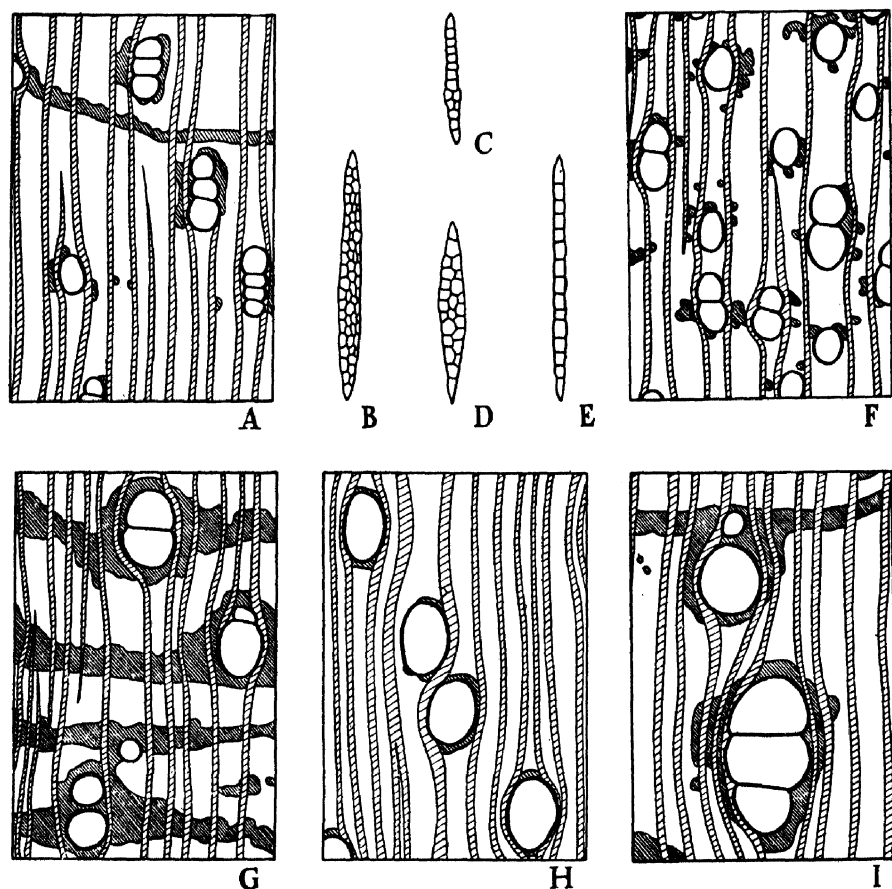


FIG. 97. SAPINDACEAE

A, *Placodiscus pseudostipularis* Radlk. B, *Sapindus mukorosi* Gaertn. C, *Ellatostachys nervosa* (F. Muell.) Radlk. D, *Blighia sapida* Kon. E, *Cubilia rumphii* Bl. F, *Schleicheria trijuga* Willd. G, *Hemigyrosa deficiens* Bedd. H, *Blighia sapida* Kon. I, *Pometia pinnata* Forst.

Sapindus, *Thouinia*, and *Thouinidium*. Perforations simple. Intervascular pitting typically alternate and very small to minute, but rather larger (up to moderate sized) in *Allophylus*, *Deinbollia*, *Dodonaea*, *Eriocoelum*, *Harpullia*, *Hippobromus*, *Lecaniodiscus*, *Placodiscus*, *Sapindus* p.p., *Schleicheria*, and *Tristira*; occasionally with distinct striations due to coalescent apertures, e.g. in *Blighia*, *Lecaniodiscus*, *Lepisanthes*, *Phialodiscus*, and *Pometia*, and, according to Solereder, in *Dodonaea*, *Koelreuteria*, *Stocksia*, and *Valenzuela*, and according to Kanehira (1206) in *Otophora alata* Blume and *Xerospermum noronhianum* Blume; pits to parenchyma similar to the intervacular pitting

except in *Deinbollia* and *Eriocoelum* p.p. in which some large oblong pits occur. Solid deposits present in nearly all the species and often abundant, gum-like and granular deposits and even crystals (*Diplokeleba* and *Lepisanthes*) often occurring together in the same wood; Janssonius (1154) refers to the presence of calcium carbonate in the vessels of certain species of *Aphania*, *Lepisanthes*, *Mischocarpus*, *Sapindus*, *Schleichera*, and *Xerospermum*; tyloses rare but recorded by Janssonius in occasional vessels of *Schleichera trijuga* Willd. and by Kanehira (1206) in *Dodonaea*, *Nephelium*, and *Pometia*. Mean member length 0.2–0.7 mm. **Parenchyma** in about 50 per cent. of the genera scanty paratracheal only (apart from terminal), often very sparse and limited to occasional cells adjoining the vessels; similar but also with crystalliferous strands scattered among the fibres in *Arytera* (1154), *Cupania*, *Euphorianthus*, *Exothea*, *Filicium*, *Koelreuteria* (1206), *Mischocarpus*, *Nephelium longana* Lam. (1206), *Pappea*, *Ratonia* (Baker 104), *Schleichera* (Fig. 97 F), *Schmidelia*, and *Stadmannia*; Heimsch (930) notes 'diffuse and diffuse-in-aggregate' parenchyma as occurring, together with abundant vasicentric types, in *Diatenopteryx*, *Elatostachys*, *Paullinia* p.p., *Serjania* p.p., *Stadmannia*, *Thouinidium*, *Toulicia*, and *Xerospermum*, and also in *Pseudina*, but with transitions to short apotracheal bands; predominantly aliform, locally confluent but without forming definite bands, in *Dodonaea*,¹ *Ganophyllum* (1154), *Hippobromus*, *Melanodiscus*, *Nephelium*, and *Placodiscus* (Fig. 97 A); similar but with crystalliferous strands scattered among the fibres in *Atalaya*, *Athyana*, *Cupaniopsis*, *Diatenopteryx* (crystals in idioblasts), *Harpullia*, and *Vouarana*; abundant, in broad confluent bands containing numerous crystalliferous strands, particularly on their margins, in *Aphania*, *Erioglossum*, *Hemigyrosa* (Fig. 97 G), *Lepisanthes*, *Meliococca*, *Octophora* (1154), *Sapindus*, *Tristiropsis*, and *Zanha*; similar but with narrower bands and without crystalliferous strands in *Diplokeleba* and *Napeodendron*. Record and Hess (1886) note broad bands also in *Dipterodendron*, *Pseudina*, and *Talisia*, though not observed by the author in the latter. Predominantly diffuse, though with abundant vasicentric parenchyma in *Toulicia guianensis* Aubl. With terminal bands in *Atalaya*, *Cupania* (938), *Exothea*, *Filicium* (938), *Glossolepis*, *Harpullia*, *Hippobromus*, *Hypelate* (938), *Melanodiscus*, *Napeodendron*, *Nephelium*, *Placodiscus*, *Podonephelium* (938), *Pometia* (938), *Sapindus*, and *Toulicia*; with terminal parenchyma only in *Paranephelium*; with idioblasts containing large single crystals in *Diatenopteryx*. Strands typically of 4 cells, but strands of 2 cells moderately common in *Athyana* and *Filicium* and predominant in *Diplokeleba* and *Hippobromus*; sometimes up to 6 or 8 cells in *Napeodendron*, *Nephelium* p.p., *Pometia*, and *Toulicia*; some fusiform cells present in *Diplokeleba* and *Hippobromus*. Storied in *Diplokeleba*. Baker (104) describes chambered crystals in *Ratonia tenax* Benth. **Rays** of most genera exclusively uniseriate or predominantly uniseriate with a few narrow biseriates; commonly biseriate in *Deinbollia*, *Eriocoelum* p.p., *Exothea*, *Filicium*, *Harpullia*, *Melanodiscus*, *Meliococca*, *Talisia*, *Tristira*, and *Zanha*, up to 3 cells wide in *Aphania*, *Diplokeleba*, *Dodonea* p.p., *Sapindus* (though sometimes up to 5 cells wide in *S. mukorosi* Gärtn. and in *S. rarak* DC. (1154)), *Schleichera* p.p., and,

¹ The material of *Dodonaea viscosa* (L.) Jacq. described by Janssonius (1154) falls into this group, but the two specimens examined by the author are typical of the main group with scanty vasicentric parenchyma only.

according to Heimsch (938) in some species of *Paullinia* and *Serjania*. Solereder records that comparatively broad rays are found in places in *Erioglossum rubiginosum* Bl. and *Serjania faveolata* Radlk. and Francis (706) notes 'aggregate' rays associated with deep indentations in *Sarcopteryx*; aggregate rays also reported (1881) in some species of *Matayba*; typically low and rarely reaching 1 mm. in height except in species of *Paullinia* and *Serjania* (938). Uniseriates often more numerous in the species with multiseriate rays than is usual with homogeneous rays and suggestive of transition to wholly uniseriate types; occasionally very few (Kribs's Homogeneous Type II), e.g. in some species of *Exothea*, *Sapindus*, and *Tristiropsis* (938); composed wholly of procumbent cells, except in the few species with heterogeneous rays. Mostly between 8 and 14 rays per mm., fewer than 4 per mm. in *Sapindus mukorosi*, 4 to 7 per mm. in *Deinbollia*, *Eriocoelum* p.p., and *Exothea*, 15 or more per mm. in *Blighia*, *Cubilia*, *Cupania*, *Diatenopteryx*, *Diploglottis*, *Diplokeleba*, *Euphoria*, *Glossolepis*, *Laccodiscus*, *Phialodiscus*, *Placodiscus*, *Schleichera* p.p., and *Stadmannia*, exceptionally numerous (20 per mm. in *Diatenopteryx*; typically homogeneous (Kribs's Types I and III, rarely II) and commonly with cells small in tangential section (about 10 μ wide tangentially), cells larger and mostly square or upright in *Cupaniopsis*, *Deinbollia*, *Glossolepis*, *Placodiscus*, and *Pometia* p.p., heterogeneous (Kribs's Types II B and III) with 1-2 marginal rows of upright cells or with occasional rows of square or upright cells interspersed among the procumbent cells, in some species of *Allophyllus*, *Cupaniopsis*, *Deinbollia*, *Eriocoelum*, *Exothea*, *Glossolepis*, *Harpullia*, *Pometia*, and *Talisia*; heterogeneous in most species of *Paullinia* and *Serjania* (938); crystals present in the ordinary cells of many species, sometimes abundant, e.g. in *Paranephelium*, *Phialodiscus*, and *Ratonia* (Baker 104), chambered crystals present in *Euphoranthus*, *Laccodiscus*, and *Stadmannia*, and with dark gum-like deposits in many species. With echelon arrangement in *Athyana*, *Cupaniopsis*, *Diatenopteryx*, *Eriocoelum*, *Erioglossum*, *Euphoranthus*, *Hippobromus*, *Lepisanthes*, *Meliococca*, *Sapindus* p.p., *Sarcopteryx*, and *Xerospermum*; storied in *Diplokeleba*. **Fibres** with simple pits, more numerous on the radial than on the tangential walls. Septate in the majority of species, the septa relatively rare or absent from some of the woods with thick-walled fibres; septa comparatively rare in *Aphania*, *Atalaya*, *Athyana*, *Doratoxylon*, *Filicium*, *Lecaniodiscus*, *Nephelium*, and *Pometia*; septa not observed in *Diplokeleba*, *Elattostachys*, *Erioglossum*, *Glossolepis*, *Guioa*, *Harpullia*, *Hemigyrosa*, *Hippobromus*, *Hypelate*, *Lepisanthes*, *Napeodendron*, *Placodiscus*, *Schleichera*, and *Stadmannia*; absent also, according to Solereder, from *Cossignia*, *Diplopeltis*, *Distichostemon*, *Lagunoa*, *Loxodiscus*, *Serjania*, *Urvillea*, and *Valenzuelia*. With thick walls in *Aphania*, *Athyana*, *Cupania* p.p., *Diplokeleba*, *Dodonaea*, *Doratoxylon*, *Filicium*, *Hemigyrosa*, *Hypelate*, *Lepisanthes*, *Napeodendron*, *Nephelium*, *Pappea*, *Paranephelium*, *Placodiscus*, and *Stadmannia*. Solereder refers to the absence of really wide lumina, cf. *Tilia*, and the consequent dense character of the woods of this family, stating, however, that relatively wide lumina occur in *Koelreuteria paniculata* Laxm., *Porocystis toulicoides* Radlk., and *Toulicia guianensis* Aubl.; to this list may be added *Jagera pseudorhus* (A. Rich.) Radlk., *Matayba ingaeifolia* Standl., and *Xerospermum glabratum* Radlk. and, according to Janssonius (1154), the septate fibres of *Guioa diplopetala* Radlk. In *Allophyllus* there is often a

tendency to form irregular, parenchyma-like bands of septate fibres with thinner walls; according to Heimsch (938), these fibres may be rounded in cross-section and with pronounced intercellular spaces. Similar bands are noted by Heimsch in *Paullinia* and *Serjania*. In *Paranephelium macrophyllum* King, the fibres are sharply segregated into 2 types, those of the early wood thin-walled, with wide lumina and numerous septa, those of the late wood thick-walled, with narrow lumina and only occasional septa; a similar distinction, though less marked, occurs in some other woods with distinct growth rings, e.g. *Sapindus* spp. Many of the species with little parenchyma have vasicentric sheaths of wide septate fibres that resemble parenchyma strands. Intercellular spaces conspicuous in some species, particularly those with thinner walls, e.g. *Jagera* and *Matayba*. Starch or gum-like substances sometimes present and occasionally abundant, e.g. *Laccodiscus*. Solereder quotes Höhnel as stating that the fibres, but not the rays, are storied in *Aphania senegalensis* (Juss.) Radlk. Mean length 0.6–1.5 mm., more than 1 mm. in *Matayba* (Kribs 1283), *Pometia*, and *Sapindus*. **Intercellular canals** observed in the rays of one specimen¹ of *Deinbollia grandiflora* Hook. f., and vertical canals of the gummosis type described by Solereder in *Dilodendron bipinnatum* Radlk. and by Record and Hess (1886) in *Diplokeleba*. **Anomalous structure**, see previous section. According to Besson (186), the wood of *Blighia sapida* Kon. has a very low silica content. The development of the **growth ring** in *Schleichera* is described by Coster (481).

TAXONOMIC NOTES

Akania, which was at one time included in this family, has been described under Akaniaceae, see p. 436.

The wood anatomy of this family is very homogeneous and is moderately highly specialized, particularly as regards the rays. Heimsch (938) places the family in a group composed of the Anacardiaceae, Burseraceae, Meliaceae, Rutaceae, Sapindaceae, and Simarubaceae and considers that there is strong anatomical evidence for believing this to constitute a natural group of plants.

Differences exist between the families, e.g. the Anacardiaceae and Burseraceae stand apart owing to the invariable occurrence of intercellular canals in the phloem and cortex, and the occurrence of septate fibres links the Sapindaceae with the Meliaceae rather than with the Rutaceae. Nevertheless, Heimsch considers that these differences are not absolute and do not serve to delimit one group from another without exceptions. He notes that the Sapindaceae are more highly specialized with respect to rays than any of the other families in this group.

Heimsch also considers that the wood anatomy, particularly the highly specialized rays, supports the view that the Aceraceae and Hippocastanaceae are close to the Sapindaceae. It should be noted, however, that these families lack septate fibres, which are characteristic of the Sapindaceae.

ECONOMIC USES

Apart from those members of the family which yield useful timbers, the fruits of various species are of economic importance. The saponin present in

¹ G. Proctor Cooper no. 357.

the tissue enables the fruits of various species of *Sapindus*, known as 'Soap-Berries', to be used for washing purposes. Other fruits such as Litchis (*Litchi chinensis* Sonn.) are edible, and sometimes sold by greengrocers in Great Britain. The Akee Apple of West Africa is obtained from *Blighia sapida* Koen. The seeds of *Paullinia cupana* Kunth. are used in Brazil for the preparation of Guarana Bread. The timbers, many of which are dense, tough, and fine-textured, are of little importance. Pearson and Brown (1679), however, include *Schleichera trijuga* Willd. and *Filicium decipiens* Thw. among the commercial timbers of India.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Alectryon,* Allophylus, Aphania, Aphanococcus, Aporrhiza, Arfeuillea, Arytera, Atalaya, Athyana, Averrhoidium, Blighia, Bridgesia, Cardiospermum, Castanospora, Chytranthus, Conchopetalum, Cossignia, Cotylo-discus, Crossonophelis, Cupania,* Cupaniopsis, Deinbollia, Diatenopteryx, Dictyoneura, Diploglottis, Diplopeltis, Distichostemon, Dodonaea,* Doratoxylon, Elattostachys, Eriandrostachys, Eriocoelum, Erioglossum, Erythrophysa, Euphoria, Exothea, Filicium, Ganophyllum, Gleniea, Gongrodiscus, Guioa, Haplocoelum, Harpullia, Hebecoccus, Heterodendron, Hippobromus, Hornea, Hypelate, Jagera, Koelreuteria,* Laccodiscus, Lecaniodiscus, Lepiderema, Lepidopetalum, Lepisanthes, Litchi, Llagunoa, Loxodiscus, Lychnodiscus, Macphersonia, Magonia, Matayba, Melanodiscus, Melicocca, Mischocarpus, Molinaea, Nephelium,* Otonephelium, Otophora, Pancovia, Pappea, Paranephelium, Paullinia,* Phialodiscus, Placodiscus, Plagioscyphus, Podonephelium, Pometia, Porocystis, Pseudima, Pseudonephelium, Rhysotoechia, Sapindus,* Sarcopteryx, Sarcotoechia, Schleicheria, Scyphonychium, Serjania,* Smelophyllum, Stadmannia, Stocksia, Storthocalyx, Synima, Talisia, Thinouia, Thouinia, Thouinidium, Tina, Toechima, Toulicia, Trigonachras, Tripterodendron, Tristira, Tristiropsis, Ungnadia, Urvillea, Valenzuela, Xanthoceras,* Xerospermum, Zollingeria.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Allophylus, Aphania, Arytera, Atalaya, Athyana, Blighia, Castanospora, Chytranthus, (Cossignia), Cubilia, Cupania, Cupaniopsis, Deinbollia, Diatenopteryx, Diploglottis, Diplokeleba, (Diplopeltis), (Distichostemon), Dodonaea, Doratoxylon, Elattostachys, Eriocoelum, Erioglossum, Euphoria, Euphorianthus, Exothea, Filicium, (Ganophyllum), Glossolepis, Harpullia, Hemigyrosa, Hippobromus, (Hypelate), Jagera, (Koelreuteria), Laccodiscus, Lecaniodiscus, Lepisanthes, (Llagunoa), (Loxodiscus), Matayba, Melanodiscus, Melicocca, Mischocarpus, Nephelium, (Otophora), Pappea, Paranephelium, Paullinia, Phialodiscus, Placodiscus, (Podonephelium), Pometia, (Porocystis), Pseudima, (Ratonia), Sapindus, Sarcopteryx, Schleicheria, (Serjania), Stadmannia, Talisia, Thouinia, Thouinidium, (Tina), (Toulicia), Tristira, Tristiropsis, Ungnadia, (Urvillea), (Valenzuela), Vouarana, Xerospermum, Zanha.

LITERATURE

(i) *On General Anatomy*

Francis 708, Guillaumin 840, Le Renard 1363, Radlkofer 1770, Sabnis 1977.

(ii) *On Wood Structure*

Baker 104, Beekman 167, den Berger 179, 182, Besson 186, Brown, F. B. H. 282, Burgerstein 310, 312, Cooper 461, Coster 481, Francis 706, Giordano 786, Greguss 2522, Heimsch 938, Holden 987, Howard 1088, Janssonius 1154, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Pearson and Brown 1679, Pfeiffer, H. 1711, 1712, Pfeiffer, J. Ph. 1713, Record 1781, 1783, 1787, 1801, 1809, 1843, 1851, 1881, Record and Hess 1886, Record and Mell 1894, Stone 2202, Torres 2269, Williams 2426, 2430, Yamabayashi 2478.

102. ACERACEAE

(FIG. 93 on p. 412; FIG. 98 on p. 434)

SUMMARY

(i) GENERAL

Trees or shrubs which occur in temperate regions in the northern hemisphere. Nearly all of the anatomical work on this family has been confined to the genus *Acer*. The **hairs** are (i) unicellular or uniseriate, with a tendency to be 2-armed in certain species; (ii) club-shaped and glandular with a uni- or biseriate stalk; (iii) transitional between (ii) and shaggy types. The leaf **epidermis** is often partly or wholly mucilaginous. **Stomata**, mostly confined to the lower surface, are ranunculaceous. **Secretory sacs**, which are most clearly visible in sections treated with eau de javelle, occur in the phloem of the leaf veins and axis, or, less frequently, in the mesophyll. In some instances they contain typical latex, but in others are filled with highly refractive contents which can be made clear by mounting dry sections in olive-oil. **Idioblasts** containing mucilage or crystals also occur in the leaf. The **crystals** are mostly solitary or clustered, but sphaerites and rod-shaped types sometimes occur as well. Smaller leaf **veins** generally vertically transcurrent. The **petiole**, in transverse sections of the few species examined, exhibits a ring of vascular bundles, enclosing medullary strands in some species.

(ii) WOOD

Vessels moderately small, with spiral thickening, perforations simple, intervacular pitting alternate and moderately large, pits to parenchyma similar; members of medium length to moderately short. **Parenchyma** in terminal bands composed mainly of fusiform cells, otherwise absent or with a few cells round the vessels or, more rarely, with diffuse chambered crystalliferous cells. **Rays** mostly 5-7 cells wide and homogeneous. **Fibres** with simple pits, moderately to very short.

LEAF

Usually dorsiventral, but sometimes tending to be centric. **Hairs** unicellular or uniseriate; 2-armed types recorded from one species of *Acer*; glandular club-shaped with a uni- or biseriate stalk together with transitions between these and shaggy forms. **Cuticle** occasionally striated; sometimes coloured white by a coating of wax on the lower surface. **Epidermis** commonly mucilaginous; papillose on the lower surface in numerous species of

Acer; including tanniniferous idioblasts on the lower side in *A. villosum* Wall. **Stomata** nearly always confined to the lower surface; sometimes rather small in diameter, recorded as infrequent on the upper side of the leaf in the region of the veins in *Acer japonicum* Thunb.; ranunculaceous. **Hypoderm** not recorded in *Acer*. **Mesophyll** generally including a single layer of palisade cells, but up to 4 layers recorded in *A. negundo* Linn. Vascular bundles of the larger **veins** usually surrounded by a ring of sclerenchyma, except in species of *Acer* belonging to the section *Indivisa* where arcs of or isolated sclerenchymatous elements occur. Small veins vertically transcurrent by thin- or thick-walled tissue in all species of *Acer*. **Petiole** (Fig. 93 D), in transverse sections through the distal end, exhibiting an adaxially flattened ring of separate bundles in all investigated species; medullary bundles sometimes present as well, e.g. in *Acer negundo*, *A. opalus* Mill., *A. rubrum* Linn. (a single medullary strand only (Plowman 1732)). Main ring of vascular bundles in the petiole surrounded by fibres in *A. campestre* Linn. and *A. opalus*, but not in *A. platanoides* Linn. Plowman records very small medullary strands in *A. saccharinum* Linn., but observed none in *A. saccharum* Marsh or *A. platanoides*. It is possible that the medullary strands are somewhat variable within a species, since they were seen to be present in a variety of *A. platanoides* examined at Kew. Watari (2365) has published a very detailed account of the petiole structure in 42 species of *Acer* from Japan and Formosa. In all of them the fundamental structure is similar to that described above, if allowance be made for complications which occur at different levels in a single petiole, especially at the apex and base. The number and size of the individual bundles both in the main outer circle and in the medullary system vary in different species. So far as the medullary bundles are concerned, these are absent from some species, extend throughout the length of the petiole in others, whilst in a third group of species they are confined to the distal end. Variations in the petiolar structure are thus of diagnostic value in the identification of species provided that comparisons are made between sections taken from the corresponding positions in each species. The petiole structure of *Acer* has, more recently, been studied by Cortesi (477) who observed medullary bundles in 6 out of the 25 species examined. Solitary and/or clustered **crystals** fairly frequent in parenchymatous tissues. Idioblasts containing small crystalline masses and a large solitary crystal, often with its long axis at right angles to the surface of the leaf, recorded in *Acer negundo* and other related species of *Acer*; often appearing as transparent dots in the leaf. Similar idioblasts, but containing clustered crystals or sphaerites, present in species of *Acer* belonging to the sections *Indivisa* and *Macrantha* as well as in *A. glabrum* Torr. **Secretory sacs**, i.e. elongated secretory cells sometimes occurring in series, stated to be always present in the phloem of the veins, and less frequently in the mesophyll of *Acer*; clearly demonstrated by treating sections with eau de javelle; containing typical latex in some instances, but with strongly refractive contents, made clear by mounting dry sections in olive-oil in others.

AXIS

YOUNG STEM (Fig. 93 G)

Cork usually superficial in origin, generally arising in the outer part of the

cortex, but more deeply seated in species secreting wax from the branches. **Cortex** containing isolated or clustered crystals in various species of *Acer*, and stone cells in *A. negundo* Linn. and *A. opalus* Mill. **Pericycle** somewhat variable; with a composite and continuous ring of sclerenchyma in *A. negundo*; with an interrupted composite ring of sclerenchyma in *A. pseudoplatanus* Linn.; with isolated strands of fibres in various other species of *Acer* as well as in *Dipteronia*. Secondary **phloem** containing bundles of sclerenchyma, which are stratified in at least certain species of *Acer*, e.g. *A. platanoides* Linn. and *Dipteronia*. Phloem in species of *Acer* and *Dipteronia* also containing groups of stone cells, chambered parenchyma containing solitary crystals, secretory sacs or cells similar to those described for the leaf. Other secretory cells with amorphous contents of a different kind, possibly mucilaginous, occur in the cortex, phloem, and pith in at least certain species of *Acer*. **Xylem** soon forming a continuous cylinder, but consisting of a circle of individually distinct bundles in transverse sections through very young stems of *Acer*. Vessels usually with simple perforations. **Pith** usually large. Stems of *A. negundo* readily giving rise to adventitious roots when in water or moist soil (Plowman 1732). **Secretory elements**, and **crystals**, see 'Cortex' and 'Phloem'.

WOOD (Fig. 98 A-B)

Vessels moderately small (50–100 μ mean tangential diameter); solitary and in multiples of 2 or 3 cells in *Acer* and with numerous clusters in *Dipteronia* (938); 30–60 per sq. mm.; with spiral thickening. Perforations simple; the smallest vessels occasionally with foraminate perforation plates. Intervascular pitting typically alternate, but, according to Heimsch (938), with not-infrequent regions of opposite pitting; sometimes moderately large, and often with hexagonal borders in *Acer*; pits to ray and wood parenchyma similar to the intervascular pitting in *Acer*, but tending to be oblong in *Dipteronia*. Usually empty; occasionally with deposits of gum; Solereder refers to deposits of calcium carbonate in *Acer rubrum* L. and '*A. illyricum*' (*A. monspessulanum* L.?), and Record (1818) mentions similar deposits in knots, bird's-eye, and dark streaks in various species. Mean member length 0.3–0.5 mm. **Parenchyma** very sparse or absent except at the boundary of the growth ring; usually with a few cells round the vessels, e.g. *A. ginnala* Maxim. and *A. pseudosieboldianum* Komar, occasionally with scattered cells containing chambered crystals, e.g. *A. macrophyllum* Pursh. and *A. opalus* Mill.; the terminal parenchyma varying from a few scattered cells to bands 1 to several cells wide and typically composed of thick-walled fusiform cells with an occasional strand divided into 2 cells, strands of 2–4 cells moderately common in a few species, e.g. *A. thompsoni* Miq. and sometimes containing crystals; strands of paratracheal parenchyma usually of 4 cells. **Rays** 2–10, mostly 5–7 cells wide, with a tendency to be of 2 distinct sizes in some species or specimens, e.g. *A. nigrum* Michx., *A. saccharum* Marsh, and *A. pseudo-platanus* L.; less than 1 mm. in height except in a few specimens, e.g. of *A. pictum* Thunb. and *A. saccharum* Marsh; with moderately numerous uniseriate composed of procumbent cells, and often only a few cells high; 3–12, mostly 6–10 rays per sq. mm.; homogeneous (Kribs's Type I) in *Acer* and composed of small cells; heterogeneous (Kribs's Type II B) to almost

homogenous in *Dipteronia* (938). Usually with gum-like contents; crystals rare, recorded (938) in *Acer oblongum* Wall. **Fibres** typically with simple pits, though narrow borders occur in a few species; pits more numerous on the

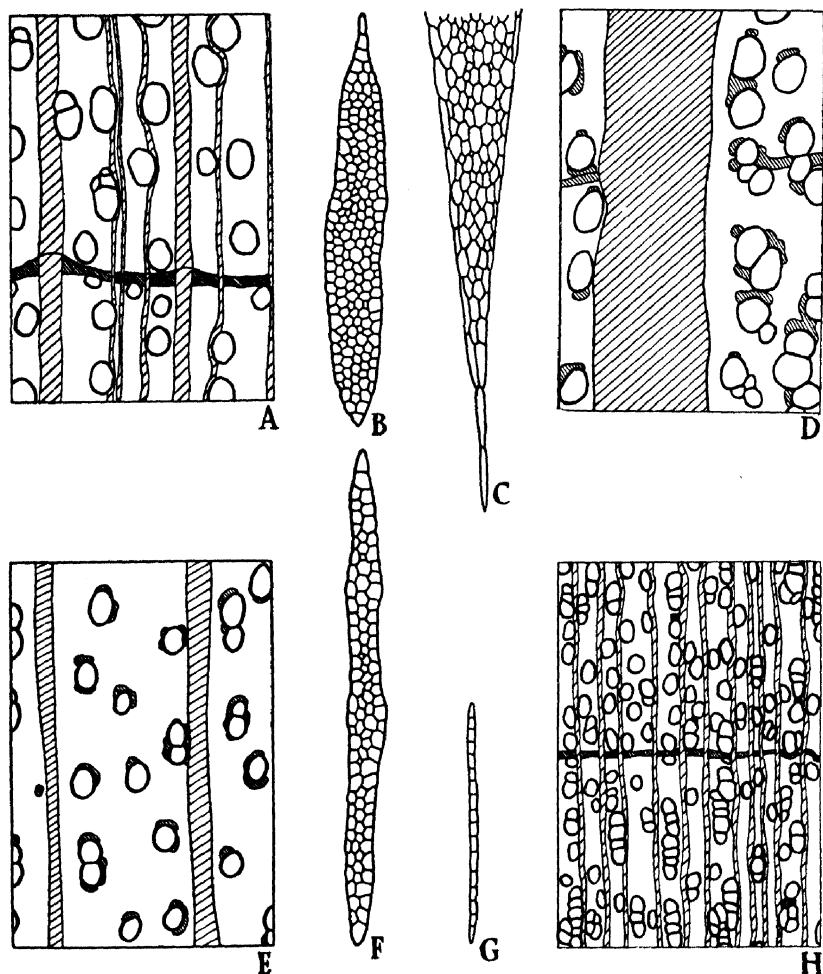


FIG. 98. ACERACEAE, A-B; AKANIACEAE, C-D; MELIANTHACEAE, E-F; HIPPOCASTANACEAE, G-H

A, *Acer saccharum* Marsh. B, *A. pseudoplatanus* Linn. C, *Akania hillii* Hook. f. D, *A. hillii* Hook. f. E, *Bersama paullinioides* Baker. F, *B. leiostegia* Stapf. G, *Aesculus hippocastanum* Linn. H, *A. hippocastanum* Linn.

radial than on the tangential walls; often with conspicuous intercellular spaces. Mean length 0.6–0.9 mm. Holden (987) has pointed out that the fibres have noticeably thicker walls in the neighbourhood of the vessels and H. P. Brown (1679) refers to elements transitional between fibre-tracheids and terminal parenchyma in the outer part of the ring of some species. Heimsch (938) states that bands or areas of starch-storing fibres are characteristic of *Acer*, but points out that they may be rendered obscure by common section-cutting

techniques. **Growth ring** formation of *Acer* in Java is described by Coster (481) and in the U.S.A. by Hanson and Brenke (888) and Lodewick (1386); the seasonal starch content and cambial activity of the stem and roots in England has been investigated by Cockerham (439).

BARK

The bark of various species of *Acer* has been investigated by Plowman (1732). Its thickness varies in different species, as also the width and degree of undulation of the medullary rays. Sclerotic elements are always present; they form definite zones in some species but are more irregularly distributed in others. *Acer platanoides* Linn. contains fewer lignified elements than the other species examined. Crystalliferous and tanniniferous cells occur in different proportions according to the species.

ROOT

Plowman (1732) has recorded the following information about the root of *A. negundo* Linn. Bark of young roots thin, containing very few sclerotic, crystalliferous, and tanniniferous cells, but including large sap-storage cells and canals. Rays numerous, straight, 1-2 cells wide. Vessels large and numerous often in radial clusters of 5. Ground tissue of the wood consisting of groups of 2 distinct sorts of tracheids with thin and thick walls respectively. Tannin abundant in old roots.

TAXONOMIC NOTES

Acer and *Dipteronia*, which are now generally regarded as members of the Aceraceae, were included in the Sapindaceae in the Bentham and Hooker system. The absence of septate fibres distinguishes these genera from the Sapindaceae, though the wood anatomy in general suggests a close relationship. Plowman (1732) has drawn attention to the morphological distinctions between *Acer negundo* Linn. and the other species of *Acer*, and, after considering these and the geological history of *A. negundo*, concludes that the species should be given generic rank with the name *Negundo aceroides* Moench. Heimsch (938), however, points out that differences in the xylem are too slight to support this change. The species is still generally known as *A. negundo*.

ECONOMIC USES

The bark of most species of *Acer* contains sugar, but in only a few of them, such as *A. saccharinum* Wang., does it occur in sufficient quantities to make its extraction possible on a commercial scale. The sap containing the sugar is obtained by tapping the trunks. The genus *Acer* furnishes some very important timbers, e.g. the Hard or Rock Maple (*A. saccharum* Marsh), Soft Maple (*A. rubrum* and *A. saccharinum*), and the Sycamore (*A. pseudoplatanus* L.). Not only is the normal straight-grained timber in demand, but the wood is often figured and highly prized for particular purposes, e.g. the curly grain or 'fiddle-back' figure for violins and 'bird's-eye' Maple for veneers.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acer,* *Dipteronia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Acer, (Dipteronia).

LITERATURE

(i) *On General Anatomy*

Cortesi 477, Hanson and Brenke 888, Plowman 1732, Sinnott 2108, Watari 2365.

(ii) *On Wood Structure*

Beekman 167, den Berger 179, Bienfait 197, Brown, H. P. 283, 288, Chalk 365, Cockersham 439, Coster 481, Desch 574, Greguss 2522, Hale 870, Hanson and Brenke 888, Heimsch 938, Hess 961, Holden 987, Holmes 1079, Howard 1088, Janssonius 1154, Jones 1191, Kanehira 1204, 1206, Lodewick 1386, Moiseeva 1545, Nicoloff 1593, Pearson and Brown 1679, Record 1778, 1783, 1818, 1843, 1851, Record and Hess 1886, Stone 2203, Tang 2231, Yamabayashi 2478.

103. AKANIACEAE

(FIG. 98 on p. 434; FIG. 99 below)

SUMMARY

A family of small trees from eastern Australia belonging to the single genus *Akania*. The following general account is based on material of *Akania hillii* Hook. grown at Kew, and the wood anatomy on a single specimen of the same

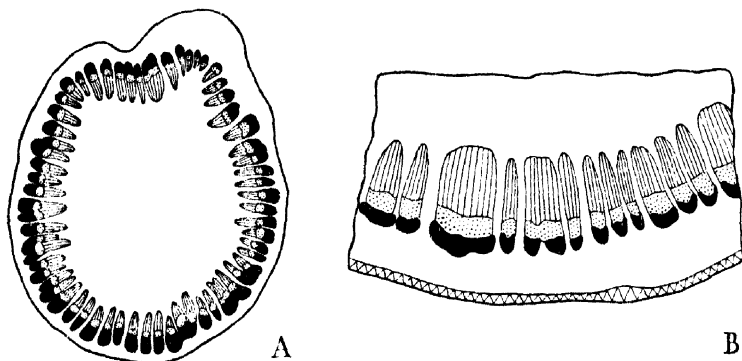


FIG. 99. AKANIACEAE

A, *Akania hillii* Hook. f. Petiole $\times 8$. B, *A. hillii* Hook. f. Portion of stem $\times 18$.

species from Australia. The wood exhibits the following characters. **Vessels** with simple or rare scalariform perforation plates, alternate to opposite intervascular pitting and elongated pits to ray cells; members of medium length. **Parenchyma** paratracheal, scanty. **Rays** very wide and high, heterogeneous, uniseriate absent. **Fibres** with bordered pits, septate, of medium length.

LEAF

Dorsiventral. **Hairs** very infrequent. Upper **epidermis** consisting of cells with slightly curved anticlinal walls; cells of the lower epidermis with more sinuous anticlinal walls. **Stomata** confined to special depressions in the lower surface of the leaf, where they occur amongst very characteristic, closely congested, slender papillae with crowned apices. **Mesophyll** including 2

layers of rather short palisade cells, but about two-thirds of its thickness is made up of very lacunar, spongy tissue. Vascular bundles of the smaller **veins** embedded in the mesophyll, each surrounded by a sheath of fibres. Vascular system in the **midrib** of the leaflets consisting of dorsal and ventral arcs of bundles, strongly supported by fibres both externally and internally, the centre of the strand being occupied by pitted cells with fairly wide lumina. **Petiole** (Fig. 99 A), in transverse sections towards the apex, exhibiting a dorsally flattened circle of individually distinct but closely packed collateral bundles, each supported by slightly less thickened fibres on the inside of each xylem group. Centre of the petiole occupied by an extensive parenchymatous tissue. Cortical region narrow. Scattered secretory cells with amorphous contents present in all unligified tissues; more frequent in the palisade than in the spongy portion of the mesophyll. Large solitary **crystals** present in some of the cells immediately external to the sclerenchymatous sheaths around the vascular bundles of the veins.

AXIS

YOUNG STEM (Fig. 99 B)

Cork arising in the sub-epidermis. **Cortex** narrow, including scattered secretory cells with amorphous contents. **Pericycle** marked by a broad, almost continuous ring of thick-walled fibres, the fibrous ring being interrupted by small groups of secretory cells opposite the medullary rays. **Xylem** and **phloem** forming individually distinct vascular bundles separated by fairly broad medullary rays. Phloem consisting of conspicuous groups of thin-walled tissue devoid of sclerenchymatous elements. Vessels solitary and variously clustered; up to about $60\ \mu$ in radial diameter; perforations mostly simple, but a few scalariform perforation plates with numerous bars also observed; sometimes with a few tyloses. **Pith** very broad, consisting mostly of pitted parenchymatous cells, but also including vertical columns of secretory cells with amorphous contents. Coarse cluster **crystals** fairly frequent in the parenchymatous tissues; only a few solitary crystals observed. **Secretory elements**, see 'Cortex', 'Pericycle', and 'Pith'.

WOOD (Fig. 98 C-D)

Vessels moderately small ($50\text{--}100\ \mu$ mean tangential diameter), solitary and in radial, tangential, or oblique multiples and clusters; about 20 per sq. mm. Perforation plates simple and moderately oblique, or very rarely scalariform. Intervascular pitting moderately small, alternate or opposite (533), pits to ray and wood parenchyma cells commonly large, horizontally elongated and simple; mean member length about $0.75\ \text{mm}$. **Parenchyma** paratracheal, limited to a few cells round the vessels, and terminal, in bands 1 or 2 cells wide. Strands mostly of 6–8 high cells. **Rays** up to 16 cells and over $400\ \mu$ wide; up to 6 mm. high; with very few or no uniseriats; about 2.5 per mm.; heterogeneous, commonly with 2–6 marginal rows of upright cells, which are often uniseriate only at the extreme tips; sheath cells present; solitary crystals present in chambered and ordinary cells. **Fibres** with numerous, small bordered pits, on both radial and tangential walls; commonly septate and with moderately thick walls; mean length about $1.5\ \text{mm}$.

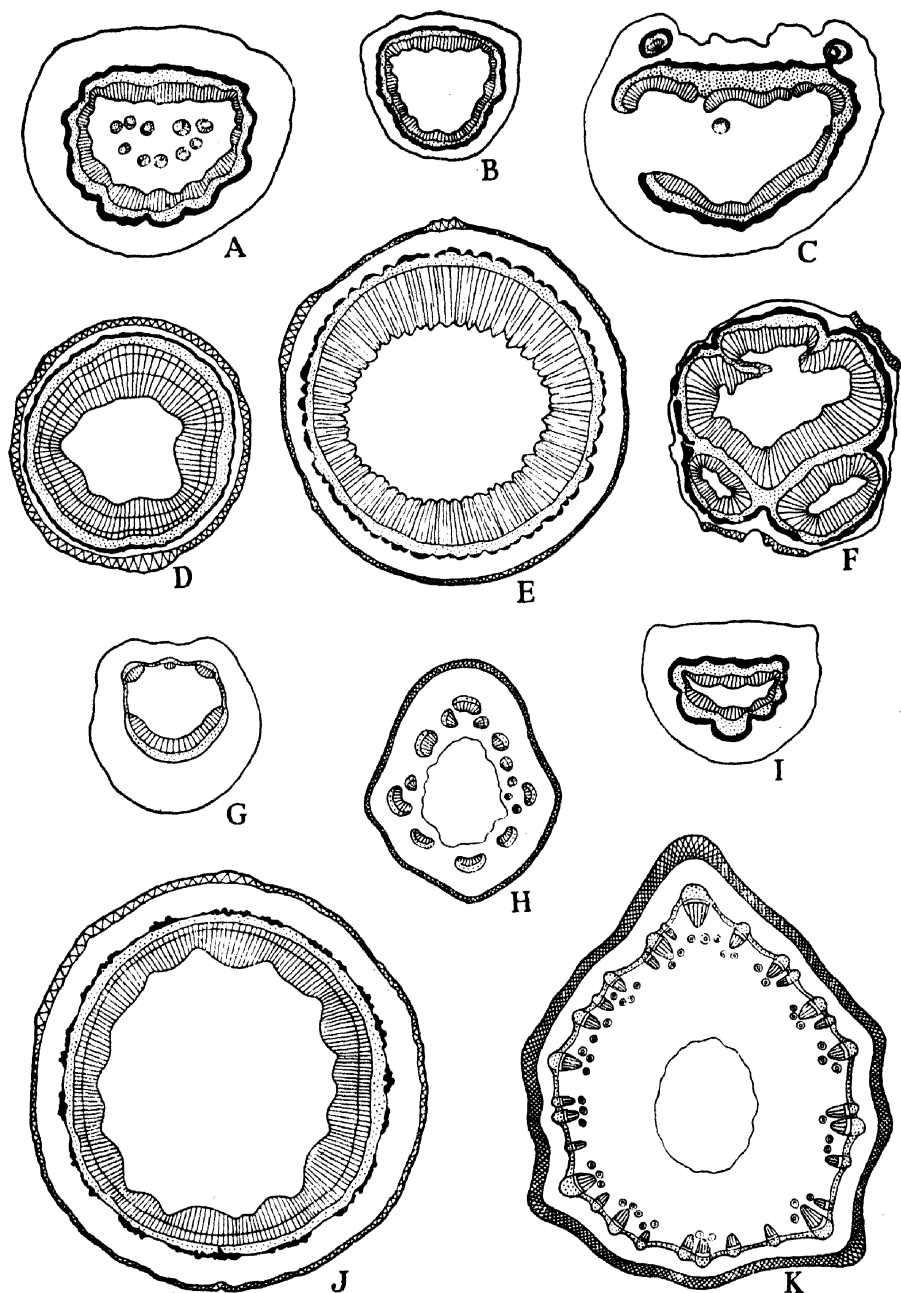


FIG. 100. HIPPOCASTANACEAE, A and E; SAPINDACEAE, B-D, F, and I;
STAPHYLEACEAE, G and J; MELIANTHACEAE, H and K

A, *Aesculus hippocastanum* Linn. Petiole $\times 6$. B, *Koelreuteria paniculata* Laxm. Petiole $\times 11$. C, *Paullinia cupana* H. B. et K. Petiole $\times 17$. D, *Koelreuteria paniculata* Laxm. Stem $\times 19$. E, *Aesculus hippocastanum* Linn. Stem $\times 7$. F, *Paullinia cupana* H. B. et K. Stem $\times 10$. G, *Staphylea holocarpa* Hemsl. Petiole $\times 19$. H, *Melanthus major* Linn. Petiole $\times 9$. I, *Xanthoceras sorbifolia* Bge. Petiole $\times 19$. J, *Staphylea holocarpa* Hemsl. Stem $\times 19$. K, *Melanthus major* Linn. Young stem $\times 9$. Small concentric circles in K represent bundles with central pith.

TAXONOMIC NOTES

The taxonomic position of *Akania* has been much discussed. *A. hillii* Hook., originally described somewhat imperfectly by J. D. Hooker, was first of all assigned to the Sapindaceae. F. Mueller and other botanists subsequently treated it as a member of the Staphyleaceae. Stapf (2185) made *Akania* the basis of a new family the Akaniaceae, and fully discussed his reasons for so doing. Harms (905) likewise treats the Akaniaceae as a distinct family. The very wide rays and the absence of uniseriates render the secondary xylem of *Akania* quite distinct from any of the woods of the Sapindaceae. For further details the articles by Stapf and Harms should be consulted.

GENUS DESCRIBED

Akania.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Harms 905, Stapf 2185.

(ii) *On Wood Structure*

Dadswell and Record 533, Heimsch 938, Record 1843, 1851.

104. HIPPOCASTANACEAE

(FIG. 100 on p. 438)

SUMMARY

(i) GENERAL

A small family of trees and shrubs consisting of the genera *Aesculus* from north temperate regions and *Billia* from tropical America. In a general way the anatomical characters resemble those of the Sapindaceae, and it will suffice to record the few characters which follow. Unicellular and uniseriate **hairs** have been recorded in both genera. The cells of the **epidermis** of the leaf sometimes have delicate, vertical, secondary walls in *Billia*, whilst, according to Solereder, mucilaginous cells are absent from the epidermis in both genera. In this last respect they differ from many of the Sapindaceae. Sclerosed cells have been recorded in the **mesophyll** in species of *Billia*. The vascular bundles of the **veins** are often vertically transcurrent in *Aesculus*. Transverse sections through the distal end of the **petiole** show a continuous cylindrical vascular strand in *Aesculus californica* Nutt. and *A. hippocastanum* Linn. (Fig. 100 A) whilst in the last species medullary bundles are present as well. Groups of stone cells have been recorded in the primary **cortex** of the young stem in species of *Billia*, whilst a composite, continuous ring of sclerenchyma in the **pericycle** is characteristic of all the species which have been examined. **Xylem** (Fig. 100 E) in the form of a continuous cylinder traversed by narrow rays. Vessels usually with simple perforations; but occasional scalariform plates also recorded. Cluster and a few solitary **crystals** observed.

(ii) Wood

Vessels small and with numerous multiples, usually numerous, perforations simple, intervacular pitting alternate, pits to parenchyma usually similar, sometimes larger or unilaterally compound, solid deposits and tyloses often present; members of medium length. **Parenchyma** (a) terminal, (b) scanty paratracheal, sometimes very sparse or absent; often storied. **Rays** exclusively uniseriate, homogeneous or weakly heterogeneous, often storied. **Fibres** with simple to distinctly bordered pits, moderately short.

AXIS

WOOD (Fig. 98 G-H)

Vessels in most species of *Aesculus* very small (less than 50 μ mean tangential diameter) to moderately small (50–100 μ); often angular, except in *Billia* (938); with numerous multiples and clusters, multiples of 4 or more cells common in most species; more than 40 per sq. mm. and often up to 70 or more; with spiral thickening in all species of *Aesculus*. Perforations typically simple, but some scalariform plates have been reported (938, 2158) in a few species of *Aesculus* and in twigs of *Billia*. Intervacular pitting typically alternate, but some opposite pitting commonly present (938); pits to ray cells often limited to the marginal rows, usually similar to the intervacular pitting, but sometimes horizontally elongated or unilaterally compound, e.g. in *A. glabra* Willd. According to Bailey (78), the sieve-like structures described by Jönsson (1192) are not true vested pits. Sometimes with solid deposits or tyloses; Record (1818) reports deposits of calcium carbonate as occasionally present in the wood of old knots. In *A. punduana* Wall. and *Billia* (1275) the vessels are larger, not angular, less numerous (10 per sq. mm.) and with fewer multiples, and Kramer (1275) distinguishes *Billia* by the absence of tyloses. Mean member length (*Aesculus*) 0.4–0.5 mm. **Parenchyma** in narrow, uni- to biseriate terminal bands in *Aesculus*, composed of strands of 4 cells that tend to be storied; the terminal bands wider in *Billia* (938); parenchyma other than terminal, absent, or very sparse, as occasional cells touching the vessels chiefly on the tangential sides. In *A. punduana* Wall. the terminal bands are up to 4 or 5 cells wide, the strands often up to 6 cells and not storied, and the parenchyma round the vessels forms a complete sheath (vasicentric). Heimsch (938) notes fusiform cells in *A. chinensis* Bunge. Solereder refers to more abundant parenchyma, often including chambered crystals, in *Billia*. **Rays** exclusively uniseriate; or with some biseriates in *Billia* (938), 10–15 per mm.; usually composed entirely of upright cells (Kribs's Homogeneous Type III), occasionally, e.g. in *A. punduana*, with single marginal rows of square or upright cells; often containing small amounts of gummy deposits. Storied in some species. **Fibres** with pits more numerous on the radial than on the tangential walls, varying from simple, e.g. in *A. punduana* Wall. to distinctly bordered, e.g. in *A. glabra* Willd. Walls thin and sometimes with a gelatinous layer. Mean length 0.6–0.9 mm.

TAXONOMIC NOTES

It is generally accepted that the Hippocastanaceae are closely allied to the Sapindaceae. Pax (1660) pointed out that it is a matter of opinion whether

they should be regarded as distinct families or whether the Hippocastanaceae should be treated as a sub-family of the Sapindaceae. Hutchinson (1113) treats the two families as one.

Heimsch (938) considers the wood anatomy to show that this family is closely related to the Sapindaceae. Both he and Tang (2233) treat *Bretschneidera* as a monotypic family closely related to the Sapindaceae, and both agree that there is no indication of real relationship between this genus and *Moringa*.

ECONOMIC USES

The timbers of a few of the species of *Aesculus* are of some commercial importance, e.g. the Ohio Buckeye, *A. glabra* Willd., and the Horse Chestnut, *A. hippocastanum* Linn., and several others are used locally for purposes requiring a fine-grained, light but fairly tough wood.

GENERA DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Aesculus,* (Billia).

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113, Pax 1660, Rehder 1903.

(ii) *On Wood Structure*

Bailey 78, Bienfait and Pfeiffer 197, Brown, H. P. and Panshin 288, 289, Chalk and Rendle 365, Greguss 2522, Heimsch 938, Holden 987, Howard 1088, Kanehira 1209, Kramer 1275, Nicoloff 1593, Record 1781, 1783, 1809, 1818, 1843, 1851, Record and Hess 1886, Stone 2203, Tang 2230, 2233.

105. MELIANTHACEAE

(FIG. 100 on p. 438)

SUMMARY

(i) GENERAL

A small family of shrubs or trees from tropical or sub-tropical Africa. The most noteworthy anatomical features include the occurrence of styloids (elongated prismatic crystals) in *Bersama* and *Melanthus* and of raphides in *Greyia*. Concentric medullary bundles occur in the axis of certain species of *Bersama* and *Melanthus*.

(ii) WOOD

Vessels rather small, perforations simple, intervacular pitting alternate and very small or scalariform to transitional (*Greyia*), pits to ray cells similar to the intervacular pitting, members moderately to very short. **Parenchyma** paratracheal, scanty, with scattered crystalliferous cells in *Bersama*; storied. **Rays** 3-9 cells wide, homogeneous or heterogeneous (*Greyia*), without uni-seriates. **Fibres** with simple pits, storied, very to extremely short.

LEAF

Dorsiventral in species of *Bersama* and *Melanthus*. Stellate hairs with 4 or more rays recorded in *Melanthus*. **Epidermis** not mucilaginous. **Stomata** confined to the lower surface; ranunculaceous. Vascular bundles of the **veins** known to be accompanied by sclerenchyma only in *Bersama abyssinica* Fres. **Petiole** (Fig. 100 H) of *Melanthus major* Linn. hollow and exhibiting, in transverse sections, a circle of vascular bundles. Small accessory bundles, similar to the medullary bundles of the stems, present on the inside of the main ring of bundles in the same species. Medullary bundles also recorded in the petiole of *Bersama abyssinica* Fres. **Styloids** lying parallel to the surface of the leaf, often situated at the boundary between the palisade and spongy mesophyll, present in *Bersama* and *Melanthus*.

AXIS

YOUNG STEM (Fig. 100 K)

Cork arising in the middle of the cortex or immediately on the outside of the phloem; composed of cells with wide lumina and delicate walls in *Greyia* and *Melanthus*, but with the outer tangential walls sclerosed in *Bersama*. Outer part of the primary cortex of *Melanthus major* Linn. composed of small thick-walled cells and the inner part of much larger, thin-walled parenchymatous cells. **Pericycle** somewhat collenchymatous in *Melanthus*; including strands of fibres, some having wide lumina and delicate transverse walls in *Bersama*, or somewhat elongated sclerenchymatous elements intermediate between parenchyma and prosenchyma in *Greyia*. Secondary **phloem** consisting wholly of soft tissue. **Xylem** in *Melanthus major* (Fig. 100 K) consisting of a circle of widely spaced bundles when very young, but soon forming a continuous cylinder; vessels in the same species exhibiting well-developed spiral thickening; perforations simple. Concentric **medullary bundles**, each consisting of a central strand of soft phloem surrounded by a ring of simple-pitted, occasionally septate, wood fibres, the strand rarely including isolated vessels, in *Bersama abyssinica* Fres. and *Melanthus major*. Medullary bundles originate at the nodes as branches from the normal bundle ring extending into the pith. **Styloids** recorded from the primary cortex, phloem and pith of *Bersama* and *Melanthus*; raphides and/or clustered crystals occur in the corresponding tissues in *Greyia*.

WOOD (Fig. 98 E-F)

Vessels moderately small (50–100 μ mean tangential diameter) in *Bersama*, very small in *Melanthus* (2158); solitary and in multiples of 2 or 3 cells; about 30 per sq. mm.; spiral thickening reported by Solereder and by Heimsch (938) in *Melanthus comosus* Vahl. Perforations simple. Intervascular pitting alternate, very small and commonly with striations due to coalescent apertures in *Bersama*, rather larger in *Melanthus* (938), scalariform and transitional in *Greyia*; pits to ray and wood parenchyma similar to the intervacular pitting. Tyloses present in *Greyia* (938). Mean member length 0.2–1.3 mm. **Parenchyma** paratracheal, rather sparse; sometimes with uniseriate vasicentric sheaths in *Bersama* and also with some scattered fusiform cells with a crystalline substance. Dadswell and Record (533) note some diffuse parenchyma also in *Greyia*. Strands of the vasicentric parenchyma usually of

2 cells but sometimes with some fusiform cells. Storied. **Rays** 3-5 cells wide in *Bersama*, up to 7-9 cells in *Greyia*; more than 1 mm., and several stories high; with few or no uniseriats; about 3-4 per mm.; homogeneous (Kribs's Type II) in *Bersama*, but with some sheath cells in *B. paullinioides* (Planch.) Bak.; heterogeneous and composed entirely of square and upright cells in *Greyia* and sometimes containing raphides (533). **Fibres** with numerous simple pits on all walls; Heimsch (938) records a few septate fibres in 2 species of *Bersama*; walls moderately thick to thick; storied; mean length about 0.7 mm. (0.3 mm. in a small shoot of *Greyia*).

TAXONOMIC NOTES

The genera comprising the Melianthaceae were included under the Sapindaceae in the Bentham and Hooker system. They were treated as a distinct family by Gürke (851), who regarded them as having affinities with the Sapindaceae. The same author draws attention to the rather notable difference between *Greyia* on the one hand and *Bersama* and *Melanthus* on the other. In this connexion it is interesting to note that Hutchinson (1113) has raised *Greyia* to the status of a new family the Greyiaceae in the Cunoniales whilst retaining *Bersama* and *Melanthus* in the Melianthaceae under the Sapindales. The secondary xylem of *Greyia* differs in some respects from that of *Bersama* particularly in having scalariform intervacular and vessel-parenchyma pitting, tyloses, heterogeneous rays, and occasional raphides. Heimsch (938) considers the differences sufficient to justify the segregation of the genus as a separate family, which he places next to the Melianthaceae. He finds no support for including the family in the Cunoniales.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Bersama, *Greyia*, *Melanthus*.*

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Bersama, *Greyia*, (*Melanthus*).

LITERATURE

(i) *On General Anatomy*

Gürke 851, Hutchinson 1113.

(ii) *On Wood Structure*

Dadswell and Record 533, Heimsch 938, Hess 959, Record 1843, 1851.

106. STAPHYLEACEAE

(FIG. 100 on p. 438; FIG. 101 on p. 444)

SUMMARY

(i) GENERAL

The known anatomical facts concerning the trees and shrubs belonging to this family may best be considered under the organs in which they occur. The family occurs in the Far East, Malaya, and in North and South America, &c.

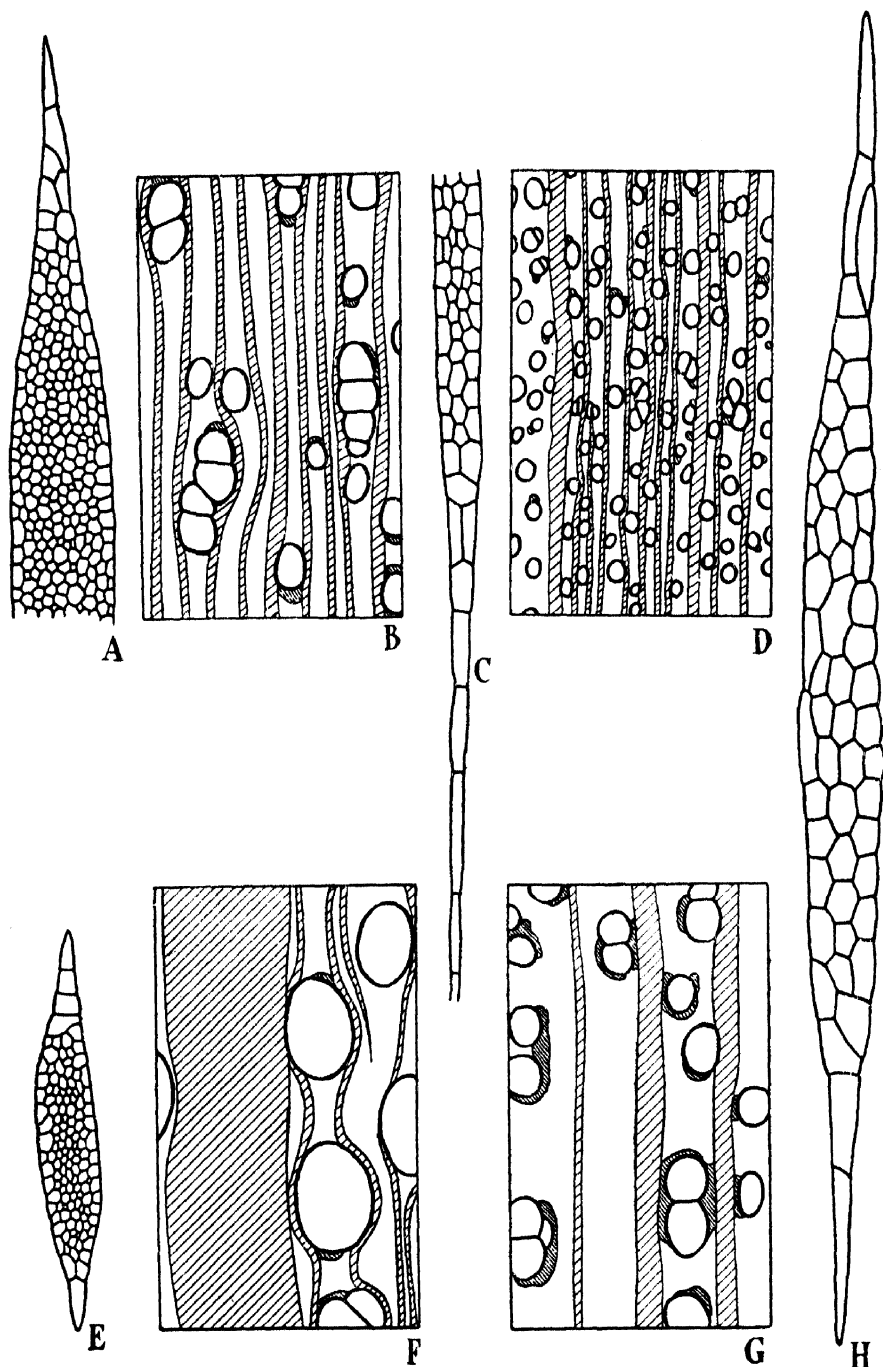


FIG. 101. STAPHYLEACEAE, A-E; SABIACEAE, F-H

A, *Euscaphis japonica* Pax. B, *Turpinia carnososa* Spruce. C, *T. pomifera* DC. D, *Staphylea bumalda* DC. E, *S. holocarpa* Hemsl. F, *Sabia paniculata* Edgew. G, *Meliosma panamensis* Standley. H, *M. panamensis* Standley.

(ii) WOOD

Vessels small, solitary, numerous, sometimes with spiral thickening, with oblique scalariform perforation plates, pits to parenchyma simple and round to oblong, sometimes with spiral thickening; members moderately to extremely long. **Parenchyma** typically paratracheal, limited to a few cells on the abaxial side of the vessels; often with a few scattered cells in addition. **Rays** mostly 4-7 cells wide and usually more than 1 mm. high, heterogeneous. **Fibres** with distinctly bordered pits, very rarely septate, moderately to extremely long. **Tracheids** often present.

LEAF

Dorsiventral. Glandular **hairs** absent. Glandular leaf teeth, composed of parenchymatous cells filled with mucilage, situated at the ends of the vascular bundles and provided with stomata on the upper surface, in *Staphylea pinnata* Linn. **Epidermis** sub-papillose on the lower surface in *Tapiscia*; upper surface mucilaginous in *Tapiscia* and *Turpinia*. **Stomata** confined to the lower surface; surrounded by 3 subsidiary cells (cruciferous type) in *Euscaphis*, *Staphylea*, *Turpinia*. **Veins** accompanied by abundant fibres in *Staphylea* and *Turpinia*; fibres absent from the corresponding position in *Euscaphis*. **Petiole** (Fig. 100 G) containing a circular vascular system, composed of a large arc of xylem and phloem towards the abaxial and 3 smaller bundles towards the adaxial side in the only 2 species of *Staphylea* examined. Clustered **crystals** present in *Euscaphis*, *Staphylea*, *Turpinia*.

AXIS

YOUNG STEM (Fig. 100 J)

Cork arising in the epidermis itself in *Euscaphis* and *Staphylea* or immediately below in *Turpinia*. **Pericycle** containing isolated strands of fibres in all examined species of *Euscaphis*, *Huerteia*, *Staphylea*, *Tapiscia*, *Turpinia*. Secondary **phloem** provided with strands of or isolated fibres in some species of *Euscaphis*, *Huerteia*, and *Turpinia*, and groups of stone cells in *Staphylea* and *Turpinia*. **Xylem** in the form of a continuous cylinder traversed by narrow rays in the 2 species of *Staphylea* examined, but individual bundles somewhat distinct immediately behind the growing-point in *S. colchica* Stev. Vessels with scalariform perforation plates. **Pith** large, consisting of thin-walled parenchyma in *Staphylea*; becoming septate owing to the disorganization of cells with mucilaginous membranes in *Tapiscia*. **Secretory cells** with amorphous (probably tanniniferous) contents in the outer part of the cortex in *Staphylea*. Only clustered **crystals** recorded in *Euscaphis*, *Staphylea*, and *Turpinia*, but solitary ones stated to occur as well in *Huerteia*.

WOOD (Fig. 101 A-E)

Vessels moderately small (50-100 μ mean tangential diameter), occasionally very small (about 40 μ), largest in *Turpinia*; typically exclusively solitary or nearly so, but with radial multiples of 4 or more cells common in some species of *Turpinia* (Fig. 101 B); varying in number from about 20 per sq. mm. in

woods with the largest vessels to about 100 per sq. mm. in woods with the smallest vessels. Sometimes with a tendency to ring-porousness in *Staphylea*; spiral thickening sometimes present in *Euscaphis* and *Staphylea* (938). Perforation plates scalariform and oblique, usually with 20–30 fine bars but with up to 50 in some species of *Turpinia*. Intervascular pitting rare owing to lack of paired vessels, opposite or transitional between scalariform and opposite; Heimsch (938) notes some alternate pitting in *Staphylea*; pits to ray and wood parenchyma commonly simple, varying from mostly round in *Euscaphis* to nearly all horizontally elongated in *Turpinia*. Contents not observed. Mean member length 1.0–2.2 mm. **Parenchyma** rather sparse, typically as a few cells along the abaxial sides of the vessels, though Holden (987) refers to it as limited to the radial walls in *Staphylea*; rather more abundant and very occasionally forming a complete sheath in *Euscaphis* and *Turpinia pomifera* DC., and with some scattered cells (diffuse) in *Euscaphis* and *Turpinia*. Strands of 4–8 cells. **Rays** mostly 4 cells wide, up to 10 cells in *Euscaphis* and some species of *Staphylea* (987); usually about 1 mm. high, but often up to 2 mm. or more in *Turpinia*; uniseriate rays numerous and composed of high upright cells, the rays themselves high in *Turpinia*; 5–15 rays per mm., least numerous in *Euscaphis* and most numerous in *Turpinia*; heterogeneous (Kribs's Types I–II A), with 4–10 rows of marginal upright cells except in *Euscaphis* (3 rows), and more than 10 rows in *Turpinia*; with sheath cells except in *Staphylea*. Crystals not observed. Perforation plates between vessels and ray cells moderately common in *Turpinia*, often reticulate. **Fibres** with numerous distinctly bordered pits on all walls, the borders of about the same size as those of the intervacular pit-pairs; Heimsch (938) records septa in *Huertia cubensis* Griseb. and *Tapiscia sinensis* Oliv. Walls moderately thin to very thick. Mean length 1.5–3.4 mm., longest in *Turpinia*. **Vasicentric** and **vascular tracheids**. Heimsch (938) refers to the occurrence, in several species, of imperforate tracheary elements that are either tracheids or fibre-tracheids; those of *Euscaphis* with spiral thickening.

TAXONOMIC NOTES

The genera included in the Staphyleaceae were treated under Sapindaceae in the Bentham and Hooker system. They are generally regarded as related to the Sapindaceae. The wood anatomy of the Staphyleaceae is very much less highly specialized than that of the Sapindaceae; there are many differences between the woods of these two families, but most of these could conceivably be accounted for by the differences in the level of specialization. Heimsch (938), however, considers the wood anatomy to be consistent with the placing of the Staphyleaceae in the Geraniales.

Commenting on Hutchinson's sub-phylum 'Pinnatae', Heimsch points out that the Staphyleaceae and Sabiaceae 'stand out among these families with prevailingly pinnately compound leaves in that they show the most primitive level of xylem organization', and concludes that in spite of the pinnate-leaved character, the family is not allied with this group.

ECONOMIC USES

Some members of the family are cultivated as ornamental shrubs.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Euscaphis, Staphylea,* Tapiscia, Turpinia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Euscaphis, (Huertea), Staphylea, (Tapiscia), Turpinia.

LITERATURE

(i) *On General Anatomy*

Pax 1659.

(ii) *On Wood Structure*

den Berger 179, 182, Chalk and Chattaway 358, Greguss 2522, Heimsch 938, Holden 987, Janssonius 1154, Kanehira 1206, Record 1783, 1843, 1851, Record and Hess 1886, Tang 2231, Williams 2430, Yamabayashi 2478.

107. DIDIEREACEAE

SUMMARY

Plants with a cactus-like habit which occur in Madagascar. The following notes concerning the structure of the leaf and stem of *Didierea* have been recorded by Solereder, whilst the description of the wood is based entirely on that of Heimsch (938).

LEAF

Mesophyll homogeneous or with a slight tendency for palisade tissue to be developed in certain species. **Stomata** infrequent, slightly depressed. **Vascular system**, in transverse sections, appearing as an almost closed arc of 7-9 bundles. Clustered **crystals** sometimes fill the cells of the epidermis. **Secretory elements**. Cells containing tannin and mucilage present in the mesophyll.

AXIS

STEM

Cortex mainly composed of parenchymatous cells with brown, tanniferous contents. Inner part of the cortex including a layer of stone cells. **Phloem** characterized by strands of fibres which appear circular in transverse sections. **Xylem** traversed by broad medullary rays; composed mainly of fibres with simple pits, but including vessels with simple perforations. Large cluster **crystals** occur in the outer part of the cortex. **Secretory elements**. Very large mucilage cavities present in the cortex.

WOOD¹

Vessels solitary and in irregular clusters and groups of multiples. Perforations simple. Intervascular pitting transitional, opposite and alternate; pits to ray cells similar. **Parenchyma** paratracheal, scanty, and terminal. **Rays** up to 4 cells wide; more than 1 mm. high; uniseriatae absent; heterogeneous. **Fibres** with simple pits.

¹ Based entirely on the description given by Heimsch (938).

TAXONOMIC NOTES

The family was included in the Sapindaceae in the Bentham and Hooker system, but doubts have frequently been expressed concerning its position there. Both Diels and Hutchinson treat the group as a separate family. Heimsch (938), from a study of the wood anatomy of *Didierea* and of a twig of *Alluaudia*, concludes that the family does not belong with the Sapindaceae.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Didierea.

(ii) FOR WOOD STRUCTURE

(*Alluaudia*), (*Didierea*).

LITERATURE

On Wood Structure

Heimsch 938.

✓ 108. SABIACEAE

(FIG. 101 on p. 444; FIG. 102 on p. 450)

SUMMARY

(i) GENERAL

A mainly tropical and sub-tropical family of woody plants, mostly included in the genera *Sabia* and *Meliosma*. *Phoxanthus* and *Ophiocaryon* each consist of only 1 species. *Meliosma* is more arboreal in habit than *Sabia*, and the leaves are much more hairy than those of the last of these genera. Le Renard (1362), who examined the stem and leaf structure of 14 species of *Sabia* and of 39 of *Meliosma*, found the structure to be fairly uniform in all important respects. In the **mesophyll** the palisade tissue of *Meliosma* differs somewhat from that of *Sabia* (see 'Leaf'), but *Sabia campanulata* Wall. was found to resemble *Meliosma* in this respect. Transverse sections through the distal end of the **petiole** in both genera show a cylindrical vascular strand slightly interrupted by ray tissue; but whereas the strand in *Meliosma* is surrounded by an almost continuous ring of sclerenchyma, in *Sabia* there is a more interrupted sclerenchymatous ring in the corresponding position. Cluster **crystals** are generally abundant in the inner cortical tissues of the petiole. The **xylem** of the young stem in both genera is traversed by fairly broad medullary rays in *Sabia* and by narrower ones in *Meliosma*.

(ii) Wood

Vessels mostly medium-sized, exclusively solitary or with some groups, perforation plates simple or simple and scalariform, and sometimes reticulate; intervacular pitting alternate, pits to parenchyma simple and often elongated; members moderately to very long. **Parenchyma** paratracheal, very to rather scanty, occasionally vasicentric. **Rays** usually up to 3-9 cells wide, sometimes up to 15-20 cells high, usually heterogeneous. **Fibres** with simple or bordered pits, sometimes septate, of medium length to moderately long.

LEAF

Dorsiventral. Rare, unicellular **hairs** recorded in *Sabia*; simple unicellular, uniseriate and glandular types with relatively long uniseriate stalks and heads of 1 or more cells occur in *Meliosma*. **Stomata** confined to the lower surface; ranunculaceous in some species, but rubiaceous in others. **Mesophyll** in *Meliosma* composed of arm-palisade cells, said by Solereder to resemble coral when folded, together with somewhat variable spongy tissue, often containing stellate cells. Arm-palisade cells not recorded in *Sabia* apart from *S. campanulata* Wall., which resembles *Meliosma* in respect of this character. Vascular bundles of the **veins** usually surrounded by sclerenchyma and accompanied externally by cluster crystals. **Petiole** of *Meliosma beaniana* Rehd. et Wils. (Fig. 102 L) exhibiting, in transverse sections through the distal end, a dorsally flattened cylindrical vascular strand, accompanied by 2 small, latero-superior bundles. Main vascular strand almost surrounded by a ring of fibres. Cluster crystals fairly abundant in the cortical tissues of the petiole, especially in a position immediately external to the main vascular strand. Petiole of *M. cuneifolia* Franch. (Fig. 102 N) similar in structure to that of the previous species, but crystals less numerous. The above petiolar structure, which was observed in material grown at Kew, appears to be common to most species of *Meliosma* and *Sabia* judging from the information recorded by Le Renard (1362). **Crystals**, see 'Petiole' and 'Veins'.

AXIS

YOUNG STEM (Fig. 102 M)

Cork always arising superficially. **Pericycle** with a composite and continuous ring of sclerenchyma in *Sabia* when sufficiently mature; isolated strands of sclerenchyma generally occur in the corresponding position in *Meliosma*. Pericyclic sclerenchyma forming an almost continuous ring in very young stems of *M. cuneifolia* Franch., but becoming more interrupted in slightly older material. **Xylem** traversed by fairly broad rays in *Sabia* and by rather narrower ones in *Meliosma*. Portions of the rays sclerosed where traversing the phloem in *Sabia*; distal portions between the phloem groups tending to be triangular in *Meliosma*. Vessel perforations mostly simple, but a proportion of scalariform plates with numerous bars also observed. Outer part of the **pith** soon becoming sclerosed in *Meliosma* and *Sabia*, or wholly lignified in *Meliosma*. Cluster **crystals** present in the cortex, phloem, and pith of *Meliosma beaniana* Rehd. et Wils. and *M. cuneifolia*, and probably in other species as well. **Secretory cells** with amorphous contents occur in the parenchymatous tissues in the same 2 species of *Meliosma*, and probably in others as well. Le Renard (1362) records them in the pith and ray cells of most species of *Meliosma*. Secretory cells, arranged in longitudinal columns, occur in the pith of *M. beaniana*.

WOOD (Fig. 101 F-H)

Vessels medium-sized (mean tangential diameter 100–200 μ) in most species; exclusively solitary in *Sabia*, solitary and in radial multiples of 2 or 3 cells in *Meliosma* and *Ophiocaryon*, and commonly in apparent tangential pairs owing to the overlapping ends of members; sometimes in irregular

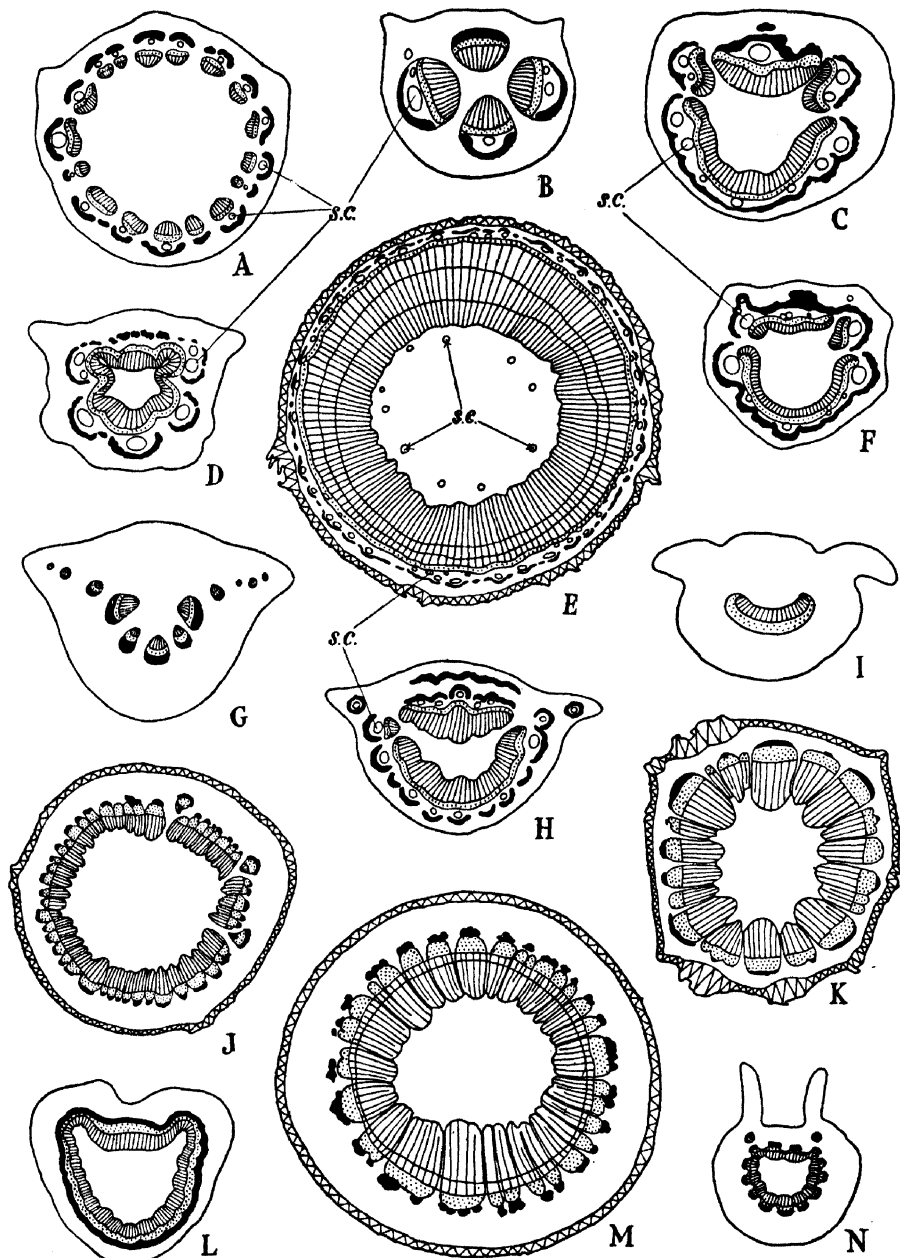


FIG. 102. ANACARDIACEAE, A-F and H; CORYNOCARPACEAE, G and J;
CORIARIACEAE, I and K; SABIACEAE, L-N

A, *Rhus trichocarpa* Miq. Petiole $\times 15$. B, *Cotinus coggygria* Scop. Petiole $\times 19$. C, *Schinus terebinthifolius* Raddi. Petiole $\times 16$. D, *Schinopsis lorentzii* (Griseb.) Engl. Petiole $\times 32$. E, *Rhus trichocarpa* Miq. Stem $\times 11$. F, *Pistacia chinensis* Bunge. Petiole $\times 19$. G, *Corynocarpus laevigata* Forst. Petiole $\times 12$. H, *Mangifera indica* Linn. Petiole $\times 14$. I, *Coriaria sinica* Maxim. Petiole $\times 12$. J, *Corynocarpus laevigata* Forst. Stem $\times 8$. K, *Coriaria sinica* Maxim. Stem $\times 8$. L, *Meliorma beamaniana* Rehder et Wils. Petiole $\times 11$. Wing bundles not shown. M, *M. cuneifolia* Franch. Stem $\times 16$. N, *M. cuneifolia* Franch. Petiole $\times 13$.

s.c. Secretory canals.

clusters; 2-10 per mm.; with spiral thickening in 1 specimen of *M. rhoifolia* Max. Perforation plates simple in *Sabia* p.p., simple and scalariform in *Meliosma* and *Ophiocaryon* and, according to Solereder, in *Sabia* p.p.; multi-perforate plates usually scalariform with few bars, but with up to 30 bars in some species, occasionally reticulate; sometimes distinctly foraminate in *M. panamensis* Standl. Intervascular pitting alternate, usually moderately large, but small in a few species; pits to parenchyma simple; large and elongated in some species. With occasional tyloses in *Meliosma* (1154) and *Ophiocaryon*. Mean member length 0.8-1.2 mm. **Parenchyma** paratracheal, scanty in *Meliosma* and very sparse or absent from *Sabia*; in narrow vasicentric sheaths and terminal bands 3-5 cells wide in *Ophiocaryon*;¹ adjacent vessels in *Meliosma* occasionally linked by a uniseriate band (1154). Strands usually of 8 cells. **Rays** usually of 2 sizes, sometimes multiserial only; the larger rays up to 3 or 4 cells wide in *Ophiocaryon*, 4-15 cells in *Meliosma*, and up to 20 cells in *Sabia*; usually more than 2 mm. high; shorter in *M. macrophylla* Merrill. and *Ophiocaryon paradoxum* R. Sch., rarely more than 3 cells wide and with a gradation of sizes; uniseriates numerous, except in *Meliosma*, and composed of square and upright cells; 3-6 rays per mm. in *Meliosma*, more numerous (9-14) in *Ophiocaryon* and *Sabia*; heterogeneous (Kribs's Types II A and II B) in *Meliosma* and *Ophiocaryon*, the cells of the large rays very variable in size and shape in different species and commonly nearly all square and upright; almost homogeneous and with distinctly procumbent cells in *M. rhoifolia* Max. and *Sabia paniculata* Edgw.; with sheath cells in most species; usually with a few cells containing dark deposits, crystals rare. **Fibres** with simple or very small bordered pits, which are more numerous on the radial than on the tangential walls, in *Meliosma* and *Ophiocaryon*, with distinctly bordered pits, which are very numerous on both radial and tangential walls and often biserial, in *Sabia*; Heimsch (938) describes the fibrous elements in *Ophiocaryon* as tracheids or fibre-tracheids; some septate fibres present round the vessels in *Meliosma* and, in some species, on the boundaries of the growth rings; Heimsch notes some septate fibres in *Sabia*. Walls thin to moderately thick. Mean length 1.2-1.9 mm. In *Meliosma* there are sometimes moderately numerous tracheid-like fibres with wide lumina and lengths equivalent to those of the vessel members.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Sabiaceae were first named the Meliosmaceae by Endlicher, and placed by him between the Hippocastanaceae and Sapindaceae. They were subsequently treated as a tribe of the Sapindaceae, but the status of a family was restored in the Bentham and Hooker system.

(ii) FROM WOOD STRUCTURE

Heimsch (938) states that in their wood structure the Sabiaceae resemble certain of the Anacardiaceae and that, if the family really belongs to the Terebinthales complex, it would seem to be closest to that family.

¹ Williams's description (2430) of *Ophiocaryon heterophyllum* Urb. differs in many respects from material examined of *O. paradoxum* Rb. Schomb., particularly as regards the parenchyma, which he records as in fine reticulate lines.

Meliosma differs from *Sabia* in several respects. There appears to be some confusion over *Ophiocaryon*, descriptions of different species showing marked divergences.

ECONOMIC USES

Some species of *Meliosma* are cultivated as ornamental trees.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Meliosma,* *Sabia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Meliosma, (*Ophiocaryon*), *Sabia*.

LITERATURE

(i) *On General Anatomy*

Dihm 589, Le Renard 1362, Warburg 2359.

(ii) *On Wood Structure*

den Berger 179, 182, Dadswell and Record 533, Heimsch 938, Janssonius 1154, Kanehira 1206, 1209, Lecomte 1334, Record 1843, 1851, Record and Hess 1886, Tang 2231, Tupper 2295, Yamabayashi 2478.

109. ANACARDIACEAE

(FIG. 102 on p. 450; FIG. 103 on p. 456)

SUMMARY

(i) GENERAL

A mainly tropical family of trees and shrubs, often resinous. The resinous substances secreted by some, but not all, of the Anacardiaceae are highly toxic and may cause severe dermatitis. One of the most notorious poisonous species is *Rhus toxicodendron* Linn., the Poison Ivy. The **hairs** are unicellular, uniseriate, and glandular, the latter being very varied in shape. The **stomata** need more complete examination, but in the few recorded instances they are stated to be ranunculaceous. The outstanding anatomical feature of the **axis** is the occurrence of **resin-canals**. These are universally present in the primary phloem, immediately on the inside of the arcs of fibres in the pericycle (see below). They are also arranged in concentric rings in the secondary phloem of older stems. Medullary resin canals have been recorded in a considerable number of genera, but similar canals in the primary cortex are much less frequent. The **cork** originates superficially. The primary **cortex**, besides the resin canals mentioned above, often includes stone cells. The **pericycle** usually contains isolated, arc-shaped strands of fibres with the convex side of each group directed towards the exterior, whilst a composite and continuous ring of sclerenchyma is much less frequent. Elongated **tannin-sacs** of varying abundance are common in the phloem throughout the family. Solitary and clustered **crystals** have been recorded.

(ii) WOOD

Vessels never very small and often moderately large, occasionally with distinct oblique or ulmiform pattern; perforation plates exclusively simple, except in 2 genera; intervacular pitting alternate, typically large, though small to minute in a few genera, with large, simple, elliptical pits to parenchyma; occasionally ring-porous and with spiral thickening. Members of medium length to moderately short. **Parenchyma** paratracheal; scanty, vasicentric or aliform and often rather sparse; with terminal or irregularly distributed broad bands in some genera. **Rays** mostly 2–3 cells wide (excluding fusiform rays containing canals) but larger in some species (up to 8–10 cells); exclusively uniseriate in a few genera; usually heterogeneous and often with few uniseriates; sometimes in echelon. **Fibres** with simple pits, septate in about half the genera; commonly with a gelatinous inner layer; of medium length to very short. **Intercellular canals** in the rays of about two-thirds of the genera.

LEAF

Dorsiventral in most species of *Rhus* of the section *Gorontogae* Engl.; consisting wholly of palisade cells in *R. incisa* Linn. **Mesophyll** in a dune form of *Rhus toxicodendron* Linn. described by Starr (2188) as having much taller palisade cells than those in mesophytic specimens of the same species. Mesophyll in *Anacardium occidentale* Linn. consisting of 2 layers of palisade cells and a broader region of spongy tissue, according to de Boer (214). Elongated sclerenchymatous cells recorded by Goris (798) in the mesophyll of *Bouea*. For particulars of the mesophyll in sumach leaves see 'Economic Uses'. **Hairs** unicellular, uniseriate, or glandular; the last of these very variable in type, recorded in *Anacardium occidentale* Linn., *Buchanania*, *Dobinea*, *Phlebociton*, and *Rhus*. Peltate glands recorded in *Camptosperma*. The following types of glandular hairs, believed possibly to be of specific diagnostic value, but requiring further investigation, recorded in *Rhus*: uniseriate with a spherical head; uni- or bicellular club-shaped glands; rosette-glands resembling stellate hairs; peltate glands, sometimes secreting sufficient resin to coat the leaves with a thin layer of varnish. A covering of deciduous hairs recorded by McNair (1474) on young leaves of *Rhus diversiloba* T. et G. Lower **epidermis** papillose in certain species of *Rhus* and *Swintonia*. Upper epidermis including mucilaginous cells in *Buchanania*. **Hypoderm** recorded by Goris (798) in *Gluta*, *Mangifera*, and *Melanorrhoea*; and a pseudo-hypoderm of divided epidermal cells in *Protorhus* by Courchet (484). **Stomata** ranunculaceous in *Anacardium occidentale* Linn., *Mangifera indica* Linn., *Rhus toxicodendron* Linn., and *Spondias lutea* Linn.; present on both surfaces or confined to the lower side in species of *Rhus* of the section *Gorontogae*; deeply sunk in *R. burkeana* Sond. **Midrib** of *Rhus toxicodendron* described by Holm (1042) as including a circular band of several collateral bundles surrounded by a sclerenchymatous pericycle. Structure of midrib similar in *Rhus glabra* Linn. Vascular bundles of the **veins** provided with resin canals in the phloem. Resin canals also occur on the upper side of the xylem in species with medullary bundles in the axis. Vascular bundles of the larger veins vertically transcurrent by fibres in *Protorhus* according to Courchet (484). Smaller veins in the same genus embedded in the mesophyll and not

accompanied by canals. **Petiole** exhibiting, in transverse sections through the distal end, an abaxial continuous arc accompanied by 1-3 adaxial groups of vascular tissue, thus giving the whole strand the appearance of a dorsally flattened but slightly interrupted ring in *Mangifera indica*, *Pistacia chinensis* Bge. (Fig. 102 F), *P. terebinthus* Linn., *Schinus terebinthifolius* Raddi. (Fig. 102 C); similar but with the ventral arc dissected into several bundles in *Cotinus americanus* Nutt. and *C. coggygria* Scop. (Fig. 102 B); with a continuous cylindrical strand having a somewhat sinuous outline in *Schinopsis lorentzii* (Griseb.) Engl. (Fig. 102 D); with a circle of numerous vascular bundles in *Rhus diversiloba* T. et G. (McNair 1474), *R. toxicodendron* (circle dorsally flattened), *R. trichocarpa* Miq. (Fig. 102 A), and *R. typhina* Linn. Petiolar vascular system with large **resin canals** in the phloem in all of the above species, and presumably throughout the family. Clustered **crystals** stated to appear as transparent dots in *Rhus succedanea* Linn., *Spondias dulcis* Forst., and the genus *Tapiria*. Solitary crystals accompany the veins in *Mangifera indica*, and clustered ones occur in the corresponding position in *Spondias lutea*. Occasional crystalliferous cells at right angles to the leaf surface recorded by Courchet (484) in *Protorhus*. Large rhombic and cluster crystals recorded by Holm (1049) in the mesophyll of *Rhus glabra* Linn. and cluster crystals in the palisade layer of *Protorhus* by Dubard and Dop (611).

AXIS

YOUNG STEM (Fig. 102 E)

Cork nearly always arising in the sub-epidermis, but rather more deeply seated in the cortex in *Campnosperma*, *Protorhus*, and *Spondias*. Cork cells with walls sclerosed on one side in *Mangifera* and *Rhus*; uniformly sclerotic on all sides in *Schinus*; thin-walled and spongy in *Odina* and *Pistacia*; tabular, with thick walls in *Astronium*; spongy but including scattered sclerosed cells in *Anacardium*. Phelloderm extensive in *Astronium* and *Pistacia*; consisting of alternate zones of stone cells and thin-walled cells in the first of these genera. Primary **cortex** containing thick-walled sclerosed cells with wide lumina in species of *Campnosperma*, *Melanorrhoea*, *Pleiogynium*, *Rhus ovata* Wats. (Watkins 2367), *Sorindeia*, and a ring of often somewhat elongated stone cells in species of *Astronium*, *Campnosperma*, *Drimycarpus*, *Haemato-staphis*, *Holigarna*, *Loxostylis*, *Mangifera*, *Pseudospondias*, *Swintonia*, *Thyr-sodium*. **Pericycle** in most species with isolated, arc-shaped strands of fibres, having the convex side towards the exterior; usually with a single, large resin-canal on the inside of each group. A composite and continuous ring of sclerenchyma present in species of *Campnosperma*, *Dracontomelum*, *Drimycarpus*, *Euroschinus*, *Gluta*, *Lithraea*, *Mauria*, *Metopium*, *Microstemon*, *Pentaspadon*, *Phlebochiton*, *Pistacia*, *Schinopsis*; and a tendency towards a composite and continuous ring in *Pseudospondias* and *Swintonia*. **Phloem** containing elongated tannin-sacs, varying in abundance in different species; chambered fibres containing solitary crystals occasionally present in the phloem in *Mangifera*, *Odina*, and *Schinus*. Secondary phloem stated to be devoid of fibres or stone cells in *Rhus*; containing stone cells but no fibres in *Pistacia*; with fibres and stone cells in *Anacardium*, *Mangifera*, *Odina*, and *Protorhus*; with fibres alone in *Schinus*. **Xylem** generally in the form of a continuous cylinder, traversed by narrow rays, but occasionally somewhat interrupted by

the primary rays; vessel perforations always simple except in a few genera (see 'Wood'). Mucilage cavities recorded in the cortex of *Campnosperma*. **Resin-canals** not only occurring immediately on the inside of each group of pericyclic fibres as mentioned above, but also present in concentric circles in the secondary phloem; stated to anastomose to form a network in species of *Rhus*, *Schinus*, and *Spondias*, and to be continuous with the canals in the rays in *Rhus viminalis* Vahl. Medullary resin-canals, varying in number in different members of a single genus or even in different internodes of a single plant, recorded in *Anacardium*, *Anaphrenium* (pro parte), *Astronium*, *Buchanania*, *Campnosperma*, *Comocladia* (pro parte), *Cyrtocarpa*, *Dracontomelum*, *Drimycarpus*, *Euroschinus*, *Faguetia*, *Gluta*, *Haematostaphis*, *Harppephyllum*, *Holigarna*, *Loxopterygium*, *Mangifera*, *Mauria*, *Melanochyla*, *Metopium*, *Microstemon*, *Odina*, *Pentaspadon*, *Phlebochiton*, *Pleiogynium*, *Poupartia*, *Pseudosmodingium*, *Pseudospondias*, *Rhus* (in tropical species), *Schinopsis*, *Schinus* (pro parte), *Sclerocarya*, *Semecarpus*, *Solenocarpus*, *Sorindeia*, *Spondias*, *Swintonia*, *Tapirira*, *Thyrsodium*, *Trichoscypha*. Cortical resin-canals much less frequent, but recorded in species of *Anacardium*, *Dobinea*, *Holigarna*, and *Thyrsodium*. **Secretory cells** with tanniniferous contents frequently abundant in the cortex, phloem, medullary rays, and pith. Solitary **crystals** (see also under 'Phloem') usually abundant, sometimes with only one type present in an individual species, but a mixture of kinds occurring in others.

Root

Each group of primary phloem containing a single resin canal; smaller canals present in the secondary phloem. Xylem of *Rhus diversiloba* T. et G. described by McNair (1474) as less firm than that of the young stem owing to the fibres being thicker and broader. Adventitious roots have been described by Buscalioni and Muscatello (320) in *Rhus viminalis* Ait. According to Holm (1042) aerial attachment roots and subterranean nutritive roots of *Rhus toxicodendron* Linn. are similar in structure, the aerial roots remaining active for only one season. Other particulars concerning root structure recorded by Weber (2380).

WOOD (Fig. 103)

Vessels mostly moderately small to medium-sized (50–200 μ mean tangential diameter), large (more than 200 μ) in some species of *Anacardium*, *Dracontomelum*, *Gluta*, *Mangifera*, *Melanochyla*, *Melanorrhoea*, *Semecarpus*, and *Spondias*, smallest in *Campnosperma*, *Nothopegia*, and *Schinus*: with an oblique pattern in *Cotinus* (1859) and *Pistacia* (Fig. 103 L), and also, though less marked, in some species of *Rhus*, ulmiform in *Schinus* (Fig. 103 P); commonly with most of the vessels solitary but with a few radial and irregular multiples of several small cells, radial multiples more common in some species of *Astronium*, *Faguetia*, *Nothopegia*, *Protorhus*, *Rhus*, and *Schinus*; varying in number from 2 to 25 per mm., fewer than 5 per mm. in most species of *Anacardium*, *Antrocaryon*, *Bouea*, *Buchanania*, *Dracontomelon*, *Gluta*, *Mangifera*, *Melanochyla*, and *Melanorrhoea*, more than 20 per mm. in *Lithraea*, *Nothopegia*, and *Schinus*; ring-porous in some or all species of *Cotinus* (1851), *Pistacia*, *Protorhus*, *Rhus*, *Schinus*, and '*Toxicodendron*' (*Rhus*) (1859); with spiral thickening in *Cotinus* (1851), *Lithraea*, *Microstemon* (938), *Pentaspadon*

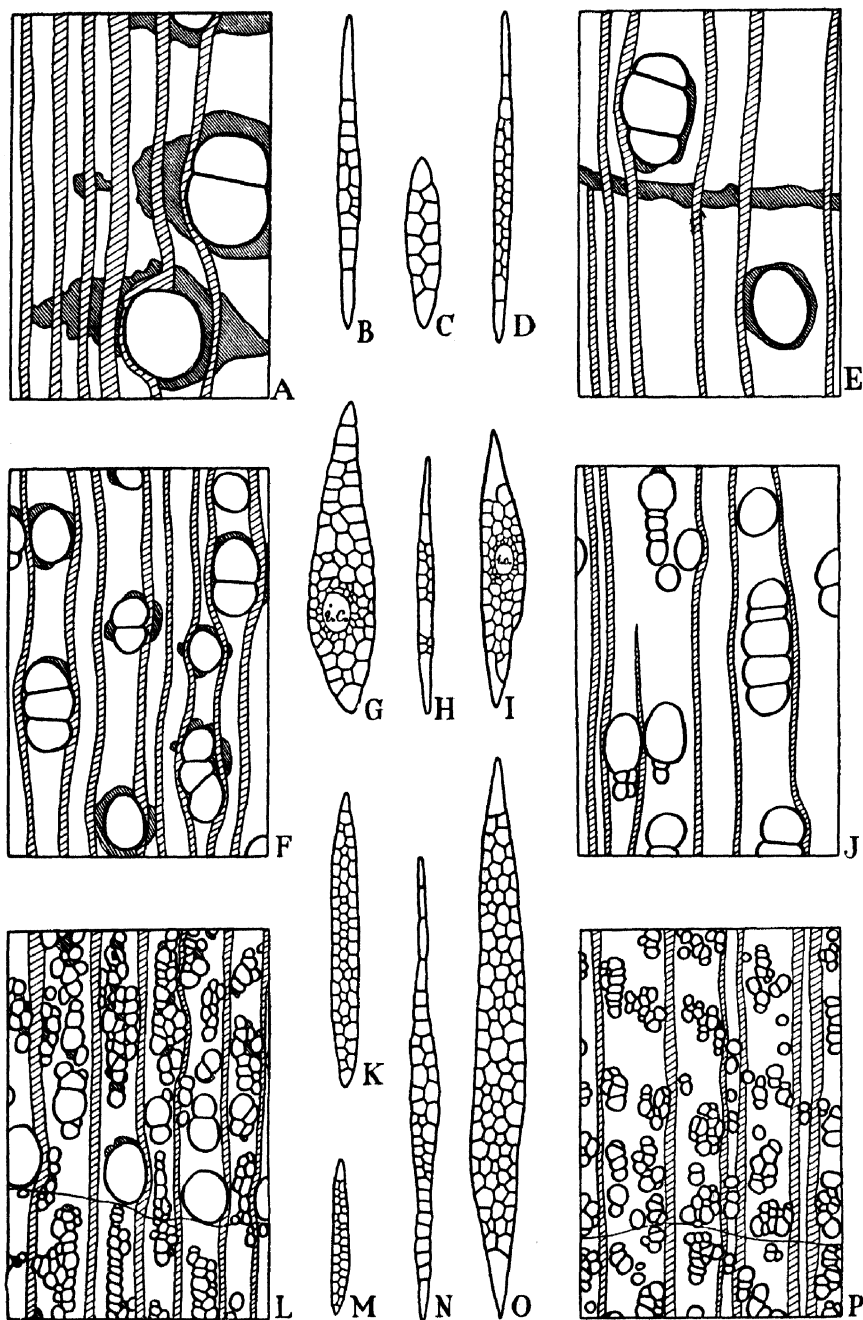


FIG. 103. ANACARDIACEAE

A, *Mangifera indica* Linn. B, '*Campnosperma wallichii* King'. C, *Mangifera indica* Linn. D, *Parishia pubescens* Hook. f. E, *Gluta travancorica* Bedd. F, *Rhodospaera rhodanthema* Engl. G, *Melanorrhoea torquata* King. H, *Microstemon velutina* Engl. I, *Lannea acidissima* A. Chev. J, *Astromium balansae* Engl. K, *Lithraea molleoides* (Vell.) Engl. L, *Pistacia terebinthus* Linn. M, *Schinus praecox* Speng. N, *Rhus integrifolia* Benth. et Hook. f. O, *Odina wodier* Roxb. P, *Schinus latifolius* Engl.
i.c. Intercellular canal.

(938), *Pistacia*, a few species of *Rhus*,¹ e.g. *R. verniciflua* Stokes, *Schinus*, *Schmaltzia* (938), and 'Toxicodendron' (*Rhus*) (1859). Perforations exclusively simple in most genera, but with a few scalariform plates in some species of *Anaphrenium* (2158), *Campnosperma*, *Heeria* (938), and *Micronychia* (2158), with fewer than 20 bars except in *Anaphrenium*. Heimsch (938) notes some modified forms of scalariform plates in species of *Comocladia*, *Euroschinus*, and *Lithraea*. Intervascular pitting alternate and typically large, rather smaller in *Buchanania* and *Loxostylis* (2158), small in *Lithraea*, *Protorhus*, *Rhus*, and *Schinopsis*, and very small in *Faguetia* and *Trichoscypha*; sometimes with striations due to coalescent apertures, e.g. in some species of *Loxopterygium*, *Melanochyla*, *Pentaspadon*, and *Rhus*; Heimsch (938) records occasional transitional types in *Campnosperma*, *Comocladia*, *Euroschinus*, and *Veatchia*, and some opposite pitting in *Dobinea*; with at least some large elliptical, simple pits where adjoining parenchyma in all the material examined, such pits usually numerous and often with the long axes horizontal and producing a scalariform appearance. Tyloses observed in most of the genera; often with dark contents. Heimsch (938) refers to sclerotic tyloses in one specimen of *Mangifera altissima* Blanco, and Janssonius (1154) notes that the tyloses may contain crystals. Mean member length 0.2–0.8 mm., mostly 0.4–0.5 mm.; longest in *Dracontomelon*. **Parenchyma** predominantly paratracheal, scanty or vasicentric, with terminal bands in some genera; often sparse in *Antrocaryon*, *Astronium*, *Blepharocarya* (525), *Buchanania*, *Comocladia*, *Dobinea* (938), *Dracontomelon*, *Euroschinus*, *Faguetia*, *Gluta* p.p., *Koordersiodendron*, *Lansea*, *Lithraea*, *Loxopterygium*, *Melanorrhoea*, *Microstemon*, *Mosquitoxylum*, *Odina*, *Parishia*, *Pentaspadon*, *Pistacia*, *Pleiogynium*, *Poupartia*, *Rhus*, *Schinopsis* p.p., *Schinus*, *Sorindeia*, *Spondias*, *Swintonia griffithii* Kurz., and *Tapirira*; aliform or locally confluent in *Anacardium*, *Holigarna*, *Mangifera*, *Melanochyla*, *Nothopegia*, *Oncocarpus*, *Protorhus*, *Schinopsis* p.p., *Semecarpus*, *Swintonia* (most species), *Thyrsodium* (1859), 'Toxicodendron' (*Rhus*) (1859), and *Trichoscypha*; transitional between banded and aliform in *Nothopegia* and some species of *Semecarpus* and *Swintonia* and with irregularly distributed broad bands, sometimes ending blindly or anastomosing, in *Bouea macrophylla* Griff., *Gluta*, *Mangifera* p.p. (938), *Melanorrhoea*, and *Metopium* (938); absent from *Campnosperma* and *Rhodosphaera*; in *Rhodosphaera* the vessels are enclosed in a sheath of thin-walled septate fibres with wide lumina, and in *Loxopterygium* similar vasicentric sheaths of septate fibres occur, but mixed with parenchyma; terminal bands 1–5 cells wide present in *Anacardium* p.p. (1859), *Bouea*, *Faguetia*, *Gluta*, *Mangifera*, *Mauria* (1859), *Melanorrhoea*, *Pistacia formosana* Mats. (1206), *Rhus* p.p., *Swintonia*, and *Trichoscypha*. Heimsch (938) notes sclerotic cells in *Mangifera altissima* Blanco. Cells commonly with dark gum-like contents; crystals very rare, except in *Lithraea* and *Mauria* (1859), in which crystalliferous strands are scattered among the fibres. Bargagli Petrucci refers to the presence of silica bodies in *Melanorrhoea obtusifolia* Engl. Strands typically of 4 cells, occasionally up to 8 cells, e.g. in *Bouea* and *Dracontomelon*. **Rays** 1–10 cells wide (excluding fusiform rays containing canals), mostly 2–3 cells; exclusively uniseriate or only occasionally biseriate in *Comocladia* (1859), *Gluta*, *Mangifera* p.p., *Melanorrhoea*, *Swin-*

¹ Record (1859) states that spiral thickening is present at least in the smaller vessels of all the American species.

tonia p.p., and *Thyrsoedium* (1859), up to 4 or 5 cells wide in at least some species of *Antrocaryon*, *Astronium*, *Buchanania*, *Dracontomelum* (1154), *Lannea*, *Lithraea*, *Metopium*, *Odina*, *Pentaspadon*, *Pistacia*, *Poupartia*, *Rhus*, *Schinopsis*, and *Schinus*, up to 8–10 cells wide in *Rhus* p.p. (1206) and *Spondias* p.p.; sometimes slightly exceeding 1 mm. in height in some species of *Dracontomelum*, *Odina*, and *Spondias*; uniseriate typically composed of both square to upright and procumbent cells, often few and usually fewer than might be expected from the degree of heterogeneity of the multiseriate rays; mostly between 5 and 10 rays per mm., fewer than 5 per mm. in *Euroschinus*, *Odina*, *Poupartia*, *Rhus* p.p., and *Spondias*, more than 10 per mm. in *Astronium*, *Bouea*, *Gluta* p.p., *Mangifera* p.p., *Nothopegia*, *Schinus*, and *Sorindeia* p.p.; heterogeneous (typically Kribs's Type II B), except in *Gluta* and *Melanorrhoea* (Kribs's Homogeneous III); rather more markedly heterogeneous in some species of *Antrocaryon* and *Campnosperma*. Usually with 1–3 marginal rows of upright cells, with 4 or more rows in *Antrocaryon*, *Holigarna*, *Microstemon*, *Rhodosphaera*, *Rhus* p.p., *Semecarpus*, and *Trichoscypha*; in some of these latter genera with markedly heterogeneous rays the biseriate parts, composed of procumbent cells, are often little wider tangentially than the uniseriate upright cells; in *Trichoscypha ferruginea* Engl. groups of procumbent cells alternate with upright cells; composed chiefly of irregular upright cells in *Dobinea* (938). Heimsch (938) notes that, apart from the rays containing canals, the rays are nearly all uniseriate and heterogeneous in a few species of *Comocladia*, *Parishia*, *Schmaltzia*, and *Sorindeia*. Cells commonly filled with a dark gum-like substance, and crystals present in many species and sometimes abundant, either in the procumbent cells or in the upright cells or, less commonly, in both; crystals in upright cells sometimes large, filling rounded cells that are slightly wider tangentially than the cells without crystals, e.g. in *Astronium urundeuva* Engl., *Koordersiodendron pinna-tum* Merrill., and *Pistacia terebinthus* L.; silica present in some species of *Melanorrhoea*, *Parishia*, and *Swintonia* (794); intercellular spaces pronounced in a few woods, e.g. *Campnosperma macrophylla* (Bl.) Hook. f., *Gluta*, and *Swintonia*; rays sometimes arranged in echelon in *Antrocaryon*, *Campnosperma*, *Euroschinus*, *Parishia*, *Rhus*, *Sorindeia*, and *Swintonia*. **Fibres** with small simple pits that are scarce on the tangential walls except in *Nothopegia*; septate in all or some species of *Anacardium*, *Antrocaryon*, *Astronium*, *Buchanania* (938), *Campnosperma*, *Comocladia*, *Dobinea* (938), *Dracontomelum*, *Harpephyllum* (938), *Koordersiodendron*, *Lannea*, *Lithraea*, *Loxopterygium*, *Mauria* (1859), *Metopium*, *Microstemon*, *Odina*, *Pleiogynium* (938), *Poupartia* (938), *Pseudospondias* (938), *Rhodosphaera*, *Rhus*, *Schinopsis*, *Schinus*, *Sclerocarya* (938), *Sorindeia*, *Spondias*, *Tapirira*, and '*Toxicodendron*' (*Rhus*) (1859); in *Loxopterygium* and *Rhodosphaera* septate fibres with wider lumina than those of the ground tissue are associated with the vessels, in the latter mixed with parenchyma (see also under 'Parenchyma'); in most species of *Buchanania* similar vasicentric septate fibres occur mixed with parenchyma, but the ground tissue is of non-septate fibres; according to Janssonius (1154) occasional septate fibres occur scattered among the non-septate fibres of the ground tissue in *Buchanania florida* Schau. and in *Mangifera*. Thin-walled in many genera but with moderately thick to thick walls in *Astronium*, *Bouea*, *Faguetia*, *Koordersiodendron*, *Loxopterygium*, *Metopium*, *Nothopegia*, *Rhodo-*

sphaera, *Schinopsis*, and *Swintonia* p.p.; very commonly with a gelatinous inner layer. Arranged in very distinct radial rows in some species of *Bouea*, *Dracontomelum*, *Melanorrhoea*, *Pentaspadon*, and *Swintonia* and some other genera, but with this feature often emphasized in the above-named genera owing to the fibres being narrower radially than tangentially. Janssonius (1154) notes the rare occurrence of solitary crystals in single specimens of *Buchanania florida* Schau. and *Spondias dulcis* Forst. var. *acida* Engl. Mean length 0.6–1.4 (mostly 0.7–1.0) mm. **Vascular tracheids** are reported by Janssonius (1154) in 2 species of *Spondias*. **Intercellular canals** occur in the rays of some or all species of *Antrocaryon*, *Astronium*, *Buchanania*, *Campnosperma*, *Euroschinus*, *Gluta*, *Harpephyllum* (938), *Koordersiodendron* (938), *Lannea*, *Loxopterygium*, *Malosma* (1859), *Melanochyla* (938), *Melanorrhoea*, *Metopium* (1859), *Microstemon*, *Odina*, *Parishia*, *Pentaspadon*, *Pistacia*, *Pleiogygium*, *Poupartia*, *Pseudospondias* (938), *Rhodosphaera*, *Rhus*, *Schinopsis*, *Schinus*, *Schmaltzia* (938), *Sclerocarya* (938), *Smodingium* (938), *Spondias*, *Swintonia*, *Tapirira*, 'Toxicodendron' (*Rhus*) (1859),¹ and *Trichoscypha*; canals very small, e.g. in *Lannea barteri* Engl., to large. The seasonal development of the **growth rings** in *Lannea* and *Spondias* has been investigated by Coster (481). Besson (186) notes a moderately high ash content and a very high silica content in the wood of *Melanorrhoea laccifera* Pierre.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Engler (628) believed the Anacardiaceae to be related to the Sapindaceae, although he pointed out that the presence of resin canals throughout the Anacardiaceae serves to distinguish this family from the Sapindaceae, where resin canals do not occur. The presence of resin canals in both the Anacardiaceae and Burseraceae has led to the suggestion that these 2 families are related, but Engler (643) disagrees with this view because of the constant floral differences between the 2 groups. It is interesting to note that Copeland and Doyel (466) wrote 'Juglandaceae are not derived from Anacardiaceae, but a collateral relationship between these families remains a possibility'.

(ii) FROM WOOD STRUCTURE

Heimsch (938) has described separately the woods of the Mangiferae, Spondiae, Rhoideae, Semecarpae, and Dobineae, but has concluded that there are no characters or combinations of characters that serve to differentiate one group from the others. There do, however, appear to be certain trends in these groups. As Heimsch has pointed out, more species of the Mangiferae have homogeneous rays and bands of parenchyma than any other, the greatest proportion of ring-porous forms with advanced stages of vessel aggregation occur in the Rhoideae, and all the species of the Spondiae have septate fibres, whereas these are lacking from the Semecarpae.

The most striking characteristics of the family—radial intercellular canals, septate fibres and paratracheal, often scanty, parenchyma—are closely paralleled in the Burseraceae. Heimsch considers that these 2 families resemble each other more closely than either family resembles the other groups covered in his study of Wettstein's Gruinales and Terebinthales.

¹ Heimsch (937), on the other hand, has been unable to confirm this.

Heimsch considers the Julianiaceae to be closely related to the Anacardiaceae. He, however, rejects Hallier's view that *Juliania* is a reduced derivative of *Pistacia* on account of the relatively highly specialized wood structure of *Pistacia*.

The evidence from wood anatomy is entirely against any relationship between the Anacardiaceae and the Juglandaceae.

Heimsch (937) has studied the secondary xylem and pollen morphology in the *Rhus* complex and his conclusions are in agreement with Barkley's taxonomic study of this complex, in which the species are grouped into the genera *Actinocheita*, *Metopium*, *Malosma*, *Cotinus*, *Toxicodendron*, and *Rhus*.

ECONOMIC USES

The resinous secretion obtained by tapping the bark of *Rhus verniciflua* Stokes, when mixed with pigments, is used in the preparation of Japanese lacquers. Sumach leaves, obtained from *Rhus coriaria* L. and certain other species of *Rhus* and *Cotinus*, are used as a source of tannin. The resin known as Mastic is obtained from *Pistacia lentiscus* Linn., while leaves of the same species are sometimes used as a substitute for Sumach. Japan wax, used in the manufacture of floor polish, &c., is extracted from the seeds of *Rhus verniciflua* Stokes. The very toxic nature of the resins secreted by some members of the family has already been mentioned in the 'summary' above. Edible fruits obtained from members of the Anacardiaceae include: the Mango (*Mangifera indica* Linn.), Cashew nuts (*Anacardium occidentale* Linn.), and Pistachio nuts (*Pistacia vera* Linn.).

Sumach leaves (*Rhus coriaria* Linn.) exhibit the following microscopical characters.

Hairs of two kinds. (a) Simple, thick-walled, pointed, usually unicellular but occasionally with a septum, often provided with an enlarged base. (b) Glandular, with a unicellular stalk and multicellular head. Upper epidermis composed of polygonal cells with almost straight anticlinal walls, covered externally with striated cuticle. Cells of the lower epidermis with thinner, more sinuous anticlinal walls. Some of the epidermal cells radiate from around the bases of the hairs. Stomata mostly confined to the lower surface; ranunculaceous. Mesophyll dorsiventral; including a single, compact layer of palisade tissue. Aggregations of cluster crystals, occasionally resembling cystoliths, present in the lacunar spongy tissue. Midrib with 3 resin canals in the phloem. Petiole in transverse sections through the distal end, exhibiting a closed, dorsally flattened vascular strand with resin canals in the phloem.

Trieste Sumach is the product of *Cotinus coggygria* Scop. Most of the microscopical characters are very similar to those of *Rhus coriaria*, but the pointed thick-walled hairs are apparently absent, although glandular hairs of the same type are common to both species. In *Cotinus coggygria* the epidermal cells on both surfaces bear hemispherical papillae, those on the lower surface being provided with finger-like processes.

The leaf of *Pistacia lentiscus*, which has been used to adulterate sumach, can be recognized by the stomata confined to the lower surface, where they are frequently surrounded by a circle of radiating epidermal cells and by the 2 or 3 layers of palisade tissue in the mesophyll. Further details have been recorded by Hanausek (882). A kind of sumach derived from *Coriaria myrti-*

folia Linn. (family Coriariaceae) can be recognized by several anatomical characters, one of the most obvious being the occurrence of rubiaceous stomata on both surfaces.

The timbers of this family range from light, colourless, and perishable to dense, highly coloured, and durable. Among the latter are the two widely known South American timbers Quebracho, *Schinopsis* spp., and Zebra Wood or Kingwood, *Astronium* spp. Some other genera, such as *Gluta* and *Melanorrhoea*, produce rather similar dense, attractively streaked timbers, e.g. the Malayan Rengas, but these do not appear to be of more than local importance. The sawdust from some species produces dermatitis. Several of the lighter timbers such as those of *Mangifera* and *Buchanania* produce non-durable general purpose timbers that are used locally and, according to Desch (574), the timber of *Campnospermum* was one of the two principle timbers used (before 1942) in the local match factories in Malaya.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Anacardium, Anaphrenium, Astronium, Botryceras, Buchanania, Campnosperma, Comocladia, Cotinus,* Cyrtocarpa, Dobinea, Dracontomelum, Drimycarpus, Euroschinus, Faguetia, Gluta, Haematostaphis, Harpephyllum, Holigarna, Lithraea, Loxopterygium, Loxostylis, Mangifera,* Mauria, Melanochyla, Melanorrhoea, Metopium, Micronychia, Microstemon, Nothopegia, Odina, Pentaspadon, Phlebochiton, Pistacia,* Pleiogynium, Poupartia, Protorhus, Pseudosmodingium, Pseudospondias, Rhus,* Schinopsis,* Schinus,* Sclerocarya, Semecarpus, Smodingium, Solenocarpus, Sorindeia, Spondias, Swintonia, Tapirira, Thyrsoodium, Trichoscypha.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Anacardium (Anaphrenium), Antrocaryon, Astronium, (Blepharocarya), Bouea, Buchanania, Campnosperma, Comocladia, Dracontomelum, Euroschinus, Faguetia, Gluta, Harpephyllum, (Heeria), Holigarna, Koordersiodendron, Lannea, Lithraea, Loxopterygium, (Loxostylis), (Malosma), Mangifera, (Mauria), Melanochyla, Melanorrhoea, Metopium, (Micronychia), Microstemon, Mosquitoxylum, Nothopegia, Odina, Oncocarpus, Parishia, Pentaspadon, Pistacia, Pleiogynium, Poupartia, Protorhus, (Pseudospondias), Rhodospaera, Rhus, Schinopsis, Schinus, (Schmaltzia), Sclerocarya, Semecarpus, (Smodingium), Sorindeia, Spondias, Swintonia, Tapirira, (Thyrsoodium), (Toxicodendron), Trichoscypha, (Veatchia).

LITERATURE

(i) On General Anatomy

de Boer 214, Brocardet 276, Buscalioni and Muscatello 320, Copeland and Doyel 466, Courchet 484, Dubard and Dop 611, Engler 628, 643, Goris 798, Hanausek 882, Holm 1042, 1049, Luthra and Sharma 1403, McNair 1473, 1474, Starr 2188, Watkins 2367, Weber 2380, Zemke 2505.

(ii) On Wood Structure

Baker 104, Benoist 170, den Berger 179, 182, Besson 186, Br. Hond. F. D. 274, Brown, F. B. H. 282, Burgerstein 310, 312, Chowdhury 411, Cooper 460, Cooper and Record 461, Coster 481, Dadswell 525, Desch 574, Fernandes 683, Foxworthy 705, Garratt 745,

Gonggrijp 794, Greguss 2522, Greiss 817, Gupta 849, Heimsch 937, 938, Hess 962, Howard 1088, Janssonius 1154, Jolly 1188, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Méniard 1491, Messeri 1493, Pearson and Brown 1679, Pereira 1687, Pfeiffer, J. Ph. 1713, Record 1780, 1783, 1787, 1801, 1807, 1816, 1825, 1843, 1851, 1859, Record and Hess 1886, Record and Mell 1894, Rendle 1913, Schmieg 2041, Stone 2202, 2207, Sudworth 2218, Tang 2231, Webber 2377, Williams 2430, Yamabayashi 2478.

110. CORYNOCARPACEAE

(FIG. 102 on p. 450; FIG. 104 on p. 470)

SUMMARY

The family consists of a few species of trees up to about 40 feet high comprising the sole genus *Corynocarpus*, which occurs in New Zealand and some of the Pacific Islands. The only species which has been described anatomically is *C. laevigatus* Forst. The wood exhibits the following characters. **Vessels** mostly in clusters, perforations simple, intervacular pitting alternate and small and pits to parenchyma similar, members moderately short. **Parenchyma** in broad, probably apotracheal, bands and vasicentric; fusiform cells common; storied. **Rays** all multiseriate, up to 16 cells wide and very high, composed of mingled rows of square and procumbent cells. **Fibres** with simple pits, of medium length.

LEAF

Dorsiventral. Globular, multicellular **hairs** occur on both surfaces of young leaves, but become disorganized and fall off when older. **Cork warts** arise in association with the bases of these hairs after abscission, according to Piggott (1719). Thread-like hairs occur on the upper surface of the stipules. **Stomata** confined to the lower surface; rubiaceous. One or 2 layers of **hypoderm** present beneath the upper epidermis, and a single layer beneath the lower epidermis. **Mesophyll** consisting of 2 layers of almost isodiametric palisade cells, not clearly differentiated from the spongy tissue which is 4 times as broad as the palisade. Vascular bundles of the **veins** embedded in the mesophyll; larger ones accompanied above and below by sclerenchymatous elements with wide lumina. Three vascular bundles enter the base of the leaf, but transverse sections through the distal end of the **petiole** (Fig. 102 G) exhibit an open arc of about 5 collateral bundles, with smaller, subsidiary, vascular strands in the wings. Large cluster **crystals** abundant in the hypoderm, especially on the upper side of the leaf; also frequent in enlarged cells in the middle of the mesophyll.

AXIS

YOUNG STEM (Fig. 102 J)

Cork arising in the outer part of the primary cortex; consisting of thin-walled cells. Primary **cortex** including groups of sclerosed cells, chiefly in the region of the lenticels. **Endodermis** not clearly differentiated. **Pericycle** containing isolated groups of fibres with rather wide lumina, situated on the outside of the phloem groups. **Xylem** and **phloem**, in transverse sections, have the appearance of a ring of individually distinct bundles, with broad lignified rays between the xylem strands. Phloem strands well developed,

devoid of resin canals and sclerenchymatous elements. Vessels tending to be in clusters or radial groups, somewhat angular, up to about $50\ \mu$ in radial diameter; perforations simple. **Pith** fairly broad, consisting of round, parenchymatous cells. Cluster **crystals** fairly numerous in the cortex, phloem, and pith; solitary prismatic crystals occur in the ray cells.

WOOD (Fig. 104 B-E)

Vessels moderately small ($50\text{--}100\ \mu$ mean tangential diameter), mostly in small multiples and irregular clusters, about 11 per sq. mm. with faint spiral thickening. Perforations simple. Intervascular pitting alternate, small; pits to ray and wood parenchyma similar to the intervacular pitting. Mean member length about $0.3\ \text{mm}$. **Parenchyma** predominantly in broad, probably apotracheal, bands, which are usually 5-10 cells wide and rather short and irregular; vasicentric parenchyma also present. Strands mostly of 2 cells, but fusiform cells common. Storied. **Rays** up to 16 cells wide, commonly more than 2 mm., and 20 stories high; uniseriate absent, about 3 rays per mm.; markedly heterogeneous, with procumbent to square or slightly upright cells intermingled, with sheath cells. Solitary crystals moderately abundant in the square cells. **Fibres** with simple pits. Walls very thick. Mean length about $1.0\ \text{mm}$.

TAXONOMIC NOTES

The taxonomic position of *Corynocarpus* has always been somewhat uncertain, the genus having been variously included in the Berberidaceae, Myrsinaceae, and Anacardiaceae. It was placed in the Anacardiaceae in the Bentham and Hooker system. In Engler's (631) opinion it belongs to the Sapindales, in which, however, it constitutes a separate family. Hemsley (949, 950), on the other hand, emphatically expressed the view that it has affinities with the Anacardiaceae, from which, in his opinion, it should not be excluded on the grounds that it is devoid of resin canals. The evidence from wood anatomy lends no support to any relationship between the Corynocarpaceae and the Anacardiaceae. The wood does, however, have many points in common with that of the Berberidaceae.

ECONOMIC USES

The fruits of *Corynocarpus laevigatus* Forst. are edible after culinary treatment, but not very palatable. They were at one time much prized by the Maoris in New Zealand. The seeds contain a poisonous substance resembling digitalin.

GENUS DESCRIBED

Corynocarpus,* (*C. laevigatus* Forst.).

* Represented in the Kew slide collection.

LITERATURE

- (i) *On General Anatomy*
Engler 631, Hemsley 949, 950, Piggott 1719.
- (ii) *On Wood Structure*
Heimsch 938.

111. JULIANIACEAE

SUMMARY

(i) GENERAL

A small family of resinous trees and shrubs consisting of the genera *Juliania* and *Orthopterygium*. It is confined to tropical America. A very thorough anatomical investigation of the family was made by Fritsch (724), using material supplied by Hemsley (951) who first established the family. Fritsch's description differs considerably from that of Jadin, which is quoted by Solereder, and he questions whether Jadin's material was correctly named. The most important anatomical character given by Fritsch is the constant occurrence of **resin canals** in the secondary phloem of the axis.

(ii) WOOD

Vessels small, perforations simple, intervascular pitting opposite to alternate, pits to parenchyma often large and elongated. **Parenchyma** paratracheal, scanty. **Rays** up to 6 cells wide, with rather few uniseriats, almost homogeneous. **Fibres** with simple pits, septate. **Intercellular canals** present in the rays.

LEAF

Usually dorsiventral. **Hairs** unicellular or multicellular, frequently forming a dense covering on the lower or both surfaces of the pinnae of the compound leaves. Various shaped glandular hairs with short stalks and more or less club-shaped heads always present as well. **Stomata** generally confined to the lower surface; ranunculaceous. **Hypoderm** absent. **Mesophyll** usually including a single layer of elongated palisade cells beneath the upper epidermis, but part of the spongy tissue towards the lower surface tends to develop into palisade in *Juliania adstringens* Schlecht. and *J. mollis* Hemsl. Spongy tissue generally occupying a smaller proportion of the mesophyll than the palisade tissue. **Veins** on the lower surface of the leaf embedded in projecting collenchymatous ribs except in *Orthopterygium*. Vascular bundles of the veins invariably include large resin canals in the phloem; not accompanied by sclerenchyma. **Petiole** of *J. adstringens* containing numerous small resin canals in the outer cortical region. Similar canals not observed by Fritsch in the corresponding position in *Orthopterygium huaucui* Hemsl. Vascular system of the petiole in the same two species appearing, in transverse sections, in the form of an arc-shaped group of vascular bundles near the base, but as a circle of bundles at the distal end. Resin canals present in the phloem of each petiolar bundle in all species, and in the pith of the petiole of *J. adstringens*. **Rachis** similar in structure to the petiole. **Crystals** exclusively clustered, mostly situated in enlarged idioblasts in the mesophyll; much smaller crystals also present in the phloem. **Secretory canals**, see 'Veins' and 'Petiole'.

Species can be distinguished by differences in the hairs and in the nature of the cuticle.

AXIS

YOUNG STEM

Structure very uniform in all species examined by Fritsch (724). **Cork**

apparently arising in the sub-epidermis; component cells usually tabular, with rather thin walls. Many cells of the initially parenchymatous primary cortex becoming more or less thickened and sclerosed except in *J. glauca* Hems. et Rose. **Phloem** invariably devoid of fibres. **Xylem** including irregularly distributed, circular vessels, 65–70 μ in diameter, mostly isolated, but sometimes in groups of 2 or 3; perforations mostly simple, but occasional scalariform plates also occur. Groundmass of the xylem composed of thick-walled fibres provided with slit-shaped simple pits, and sometimes septate by thin partitions. Rays 1–2 cells wide. Wood parenchyma generally absent except from around the primary vessels. **Pith** well developed, composed of rectangular, vertically elongated cells with simple pits. Abundant clustered **crystals** and infrequent solitary ones occur in the cortex; clusters present in longitudinal rows of parenchymatous cells in the phloem; small infrequent clusters recorded in the pith.

Details concerning the complex structure of the inflorescence as well as of the fruit and embryo can best be obtained from Fritsch's (724) paper. Variations in the distribution of **resin canals** were found by Fritsch to be of some value in the identification of species. Resin canals invariably present in the primary cortex; at least one ring of large ones in the secondary phloem; numerous small ones in the pith of all species except *J. adstringens* Schlecht. and *Orthopterygium huacui* Hemsl.

WOOD¹

Vessels small (less than 100 μ mean tangential diameter); solitary and in multiples of 2–8 cells and occasional clusters; usually 15–25 per sq. mm. Perforations simple. Intervascular pitting mostly alternate, sometimes opposite; pits to ray and wood parenchyma often large and elongated. Tyloses abundant. **Parenchyma** paratracheal, scanty. **Rays** up to 6 cells wide; uniseriate rather few and not more than 10 cells high, composed of square and upright cells; almost homogeneous (Kribs's Type I); crystals present. **Fibres** with simple pits, septate and with thin walls. **Intercellular canals** present in the rays; the epithelial layers composed of very small cells.

TAXONOMIC NOTES

In the Bentham and Hooker system, *Juliania* was placed in the Anacardiaceae. Hemsley (951) created the family Julianiaceae from the genera *Juliania* and *Orthopterygium*. While admitting that they resemble the Anacardiaceae in certain respects, he considered their affinities with the Juglandaceae and Cupuliferae to be closer. Hemsley's views were strongly disputed on anatomical grounds by Fritsch (724), who demonstrated that there is no clear-cut line of demarcation between the Julianiaceae and Anacardiaceae. Fritsch also pointed out that the suggestion made by Jadin, and quoted by Solereder, that there are affinities between the Julianiaceae and Simarubaceae, is probably based on an examination of wrongly named material. Kershaw (1234), after examining the ovules of the Julianiaceae, Juglandaceae, and Anacardiaceae, was unable to express a definite opinion concerning the affinities of the Julianiaceae, since they were found to resemble both of the families with which they were compared in certain respects.

¹ Based entirely on the literature, particularly the description by Kramer (1275).

Wettstein (2416) treats the Julianiaceae as the first family of the Juglandales, where they were also placed by Hutchinson (1113). Engler and Gilg (643 A) include them in a separate order the Julianiales, which, with the Batidales, comes between the Juglandales and Fagales. On the other hand, Heimsch (938) and Kramer (1275), working with the secondary xylem, have confirmed Fritsch's view that the Julianiaceae and Anacardiaceae are closely related to one another. Copeland and Doyel (466) also conclude that the Julianiaceae and Anacardiaceae are very closely related to one another.

It can thus be seen that there has been a cleavage of opinion between anatomists and taxonomists concerning the affinities of the Julianiaceae. In view of Fritsch's demonstration that the anatomical evidence is very heavily loaded in favour of the Julianiaceae being related to the Anacardiaceae, whilst they are anatomically unlike the Juglandaceae, the family is placed next to the Anacardiaceae in this book.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Juliania, Orthopterygium.

(ii) FOR WOOD STRUCTURE

(Juliania), (Orthopterygium).

LITERATURE

(i) *On General Anatomy*

Copeland and Doyel 466, Engler and Gilg 643 A, Fritsch 724, Hemsley 951, Hutchinson 1113, Kershaw 1234, Wettstein 2416.

(ii) *On Wood Structure*

Heimsch 938, Kramer 1275, Record 1851, Record and Hess 1886, Webber 2377.

112. CORIARIACEAE

(FIG. 102 on p. 450)

SUMMARY

A family consisting of shrubs from temperate regions, belonging to the single genus *Coriaria*. The wood exhibits the following characters. **Vessels** commonly grouped tangentially, sometimes ring-porous, perforations simple; intervacular pitting alternate, small; pits to parenchyma similar, sometimes oblong; members very short. **Parenchyma** paratracheal, scanty, vasicentric or confluent, storied. **Rays** up to 15 cells wide and without uniseriatae. **Fibres** with simple pits, moderately to very short.

LEAF

The lamina has been most fully investigated (Wiesner 2423, p. 904) in *Coriaria myrtifolia* Linn. which exhibits the following characters. Dorsiventral. Cells of the upper **epidermis** polygonal, somewhat angular; those of the lower epidermis more irregular, provided with pitted anticlinal walls and covered externally by striated cuticle. **Stomata** present on both surfaces, but most numerous on the lower side; rubiaceous, but with well-developed

cuticular striations at right angles to the pore. **Mesophyll** including 2 layers of palisade cells. Vascular bundle of the **midrib** surrounded by collenchyma. **Petiole** of *Coriaria sinica* Maxim (Fig. 102 I) grown at Kew exhibiting, in transverse sections through the distal end, a solitary, open, arc-shaped vascular strand, not supported by pericyclic sclerenchyma. Infrequent cluster **crystals** present in the cortical region of the petiole in the same species. Solitary monoclinic **crystals**, as well as crystalline concretions with a corroded appearance, present in all parts of the mesophyll of *C. myrtifolia*. All cells in the same species coloured blue on treatment with ferric chloride solution. Needles of gypsum deposited on the addition of dilute sulphuric acid. The mesophyll is coloured brownish-red, and a similarly coloured precipitate formed on applying caustic soda solution, especially following a preliminary treatment with alcohol.

AXIS

YOUNG STEM (Fig. 102 K)

The following details refer particularly to *Coriaria sinica* Maxim grown at Kew. **Cork** arising in the sub-epidermis. Primary **cortex** narrow, consisting of rounded, somewhat spongy, parenchymatous cells. **Pericycle** containing a few large strands of fibres. Primary **phloem** forming well-developed strands, containing no sclerosed elements. **Xylem** in the form of a cylinder, traversed by broad primary medullary rays, the latter being lignified between the xylem groups. Vessels mostly in irregular clusters, the individual elements varying considerably in size and shape as seen in transverse sections, up to about 100 μ in radial diameter; perforations simple, somewhat oblique. **Pith** fairly broad. Infrequent cluster **crystals** present in the pith, and occasional solitary ones in the ray cells.

WOOD¹

Vessels small (mean tangential diameter less than 100 μ); mostly solitary or mostly in multiples and clusters that often extend tangentially; occasionally ring-porous. Perforations simple. Intervascular pitting alternate and small; often with coalescent apertures; pits to ray and wood parenchyma similar, sometimes with a few oblong pits. Mean member length about 0.2 mm. (1206). **Parenchyma** paratracheal, about the vessel groups and often linking them; rather sparse in species with mostly solitary vessels, forming broad, irregular confluent bands in others. Fusiform cells present. Storied. **Rays** up to 15 or more cells wide and often more than 4 mm. high; uniseriate absent; composed almost entirely of square to upright cells; with sheath cells and crystals. **Fibres** with simple pits; mean length about 0.6–0.8 mm.

TAXONOMIC NOTES

In the Engler system the Coriariaceae are included in the Sapindales and placed near the Anacardiaceae. In the Bentham and Hooker system they are also placed next to the Anacardiaceae. They resemble the Anacardiaceae in containing abundant tannin, but differ from them in several important details, such as the absence of resin canals and the possession of rubiaceous stomata.

¹ Based entirely on the literature.

Hutchinson (1113) treats the Coriariaceae as the sole family in the Coriariales, which he believes to have no connexion with the Anacardiaceae.

The wood structure lacks two of the features most characteristic of the Anacardiaceae, the septate fibres and radial intercellular canals; neither of these features, however, is constant throughout that family. The type of ray in the Coriariaceae is very different from that found in the Anacardiaceae. Heimsch (938) states: 'It seems doubtful, because of the extreme specialization of the wood rays, that these families', i.e. Corynocarpaceae and Coriariaceae, 'belong with those forming the nucleus of Wettstein's Terebinthales.'

ECONOMIC USES

The leaves of *Coriaria myrtifolia* Linn. are sold as a source of tannin. In this respect they strongly resemble those of sumach (*Rhus coriaria* Linn.). (See Anacardiaceae, 'Economic Uses'.)

GENUS DESCRIBED

(*Coriaria*.)*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Casparis 345, Hutchinson 1113, Wiesner 2423.

(ii) *On Wood Structure*

Dadswell and Record 533, Heimsch 938, Kanehira 1206, Record 1843, 1851, Record and Hess 1886.

113. MORINGACEAE

(FIG. 104 on p. 470)

SUMMARY

The family consists of trees with an Acacia-like habit belonging to the single genus *Moringa*, of which there are only a few species. They occur in India, North Africa, &c. The following description of the leaf and stem structure is largely based on that by Durin (618). One of the most significant anatomical features is the presence of **myrosin cells**, which occur in the mesophyll of the leaf as well as in the cortex and phloem of both stem and root. **Vessels** of the mature wood medium-sized, with numerous multiples of 3 or 4 cells, perforations simple, pits to parenchyma large and often simple; members moderately short. **Parenchyma** paratracheal vasicentric or slightly aliform, strands of 2-4 cells, storied. **Rays** 2-3 cells wide, about 8 per mm., homogeneous, storied. **Fibres** with large simple pits on the radial walls, storied, moderately short.

LEAF

Compound. Leaflets exhibiting the following characters. Dorsiventral. **Hairs** unicellular, with blunt tips. Cells of the **epidermis** said to be mucilaginous in *M. aptera* Juss. **Stomata** ranunculaceous. **Mesophyll** partly composed of well-developed palisade tissue which forms a continuous layer from one margin to the other in *M. pterygosperma* Gaertn., but is interrupted

by collenchyma above the main vein in *M. concannensis* Nimmo. **Midrib** in *M. pterygosperma* containing a crescentic strand of xylem and phloem, accompanied above and below by collenchyma. **Starch**, **myrosin**, and **cluster crystals** of calcium oxalate abundant.

AXIS

YOUNG STEM

The following description applies mainly to *M. pterygosperma* Gaertn. except where stated. **Cork** narrow. **Cortex** parenchymatous, but including strands of sclerenchyma towards the phloem (probably pericyclic sclerenchyma). A continuous ring of fibres also occurs, except in very young stems, nearer the periphery of the cortex. **Phloem** consisting of very small cells. **Xylem** in the form of a cylinder traversed by rays up to 3 cells wide; largely composed of radial groups of vessels and fibres respectively. Vessels with simple perforations. **Pith** chiefly consisting of parenchymatous cells, but including a large, central mucilage canal, lined with epithelial tissue, and sometimes accompanied by a second, smaller canal. **Starch** and **myrosin** abundant in the cortex. **Cluster crystals** also numerous in the parenchymatous tissues, especially in the portions of the rays between the phloem groups. The general structure is similar in other species of *Moringa* apart from small variations in the amount of starch, the distribution of sclerenchyma, and other minor features.

WOOD (Fig. 104 A and D)

Vessels medium-sized (100–200 μ mean tangential diameter); commonly with numerous multiples of 3 or 4 cells and occasionally more; 1.5–12 per sq. mm. Perforations simple. Intervascular pitting alternate, large; pits to wood and ray parenchyma large, simple or slightly bordered and sometimes elongated horizontally. Contents not observed. Mean member length 0.25–0.3 mm. **Parenchyma** paratracheal, vasicentric or sometimes slightly aliform. In some species the parenchyma includes areas of very thin-walled spongy tissue (Lücken), which may also include parts of the rays. Sometimes containing single crystals in the ordinary cells; strands of 2–4 cells, with a few fusiform cells in some species. Storied. **Rays** 2–3 cells wide and low; uniseriates very few in some species, composed of procumbent cells; about 8 per mm.; homogeneous (Kribs's Types I–II). Cells sometimes containing single crystals. Storied. **Fibres** with large lenticular, simple pits, numerous on the radial walls but rare on the tangential. Walls thin to moderately thin. Markedly 'bauchig'. Storied. Mean length 0.75–1.0 mm. **Intercellular canals** of the vertical traumatic type reported by Record (1801). **Growth rings**. The seasonal development of the wood has been investigated by Coster (481).

ROOT

Tuberous when young, but becoming branched when mature. **Cork** broad even in young roots, consisting of rectangular cells in radial rows. **Cortex** parenchymatous, but including numerous groups of sclerenchymatous elements in the outer part. The xylem of *M. concannensis* Nimmo occurs

in individually distinct vascular bundles, but is more continuous in *M. pterygosperma* Gaertn.; including vessels of various sizes, irregularly distributed, or, less frequently, exhibiting a radial arrangement. **Pith** generally absent from *M. pterygosperma*, but a small amount present in *M. concannensis*. **Starch** and

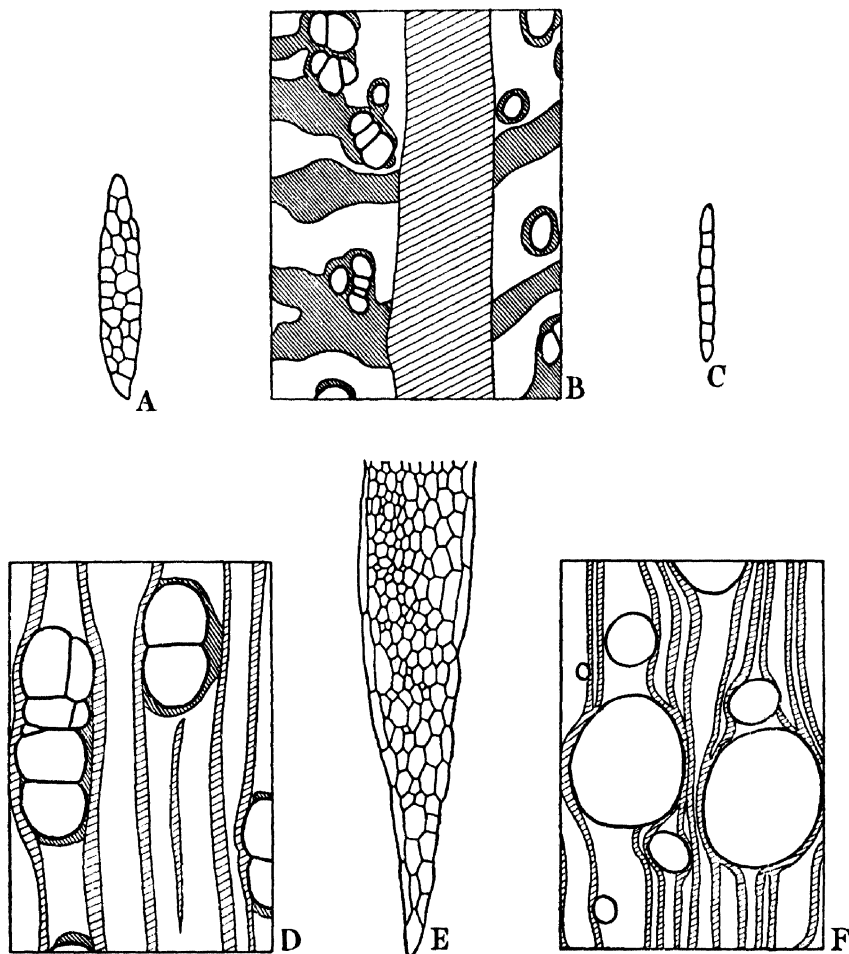


FIG. 104. MORINGACEAE, A and D; CORYNOCARPACEAE, B and E;
CONNARACEAE, C and F

A, *Moringa pterygosperma* Gaertn. B, *Corynocarpus laevigata* Forst. C, *Manotes macrantha* Schellenberg. D, *Moringa pterygosperma* Gaertn. E, *Corynocarpus laevigata* Forst. F, *Manotes macrantha* Schellenberg.

myrosin abundant in the cortex; cluster **crystals** widely distributed in the parenchymatous tissues.

TAXONOMIC NOTES

The possession of myrosin cells indicates the existence of affinities with the Capparidaceae, Resedaceae, and Cruciferae, and thus supports the position

to which the family is assigned in the respective systems of Engler and Hutchinson.

ECONOMIC USES

M. pterygosperma Gaertn. is known as the Horse-radish Tree, and is commonly cultivated in India and adjacent countries as well as in the West Indies. The presence of myrosin gives the roots the flavour of horse-radish. The fruits are edible, and the seeds yield an oil which has been used for lubricating delicate machinery.

GENUS DESCRIBED

Moringa.

LITERATURE

(i) *On General Anatomy*

Durin 618, Pax 1661.

(ii) *On Wood Structure*

den Berger 182, Coster 481, Janssonius 1154, Record 1801, 1809, 1851.

114. CONNARACEAE

(FIG. 104 on p. 470; FIG. 105 on p. 472)

SUMMARY

(i) GENERAL

All members of this tropical family are woody, but they exhibit a considerable diversity of habit. The genera *Ellipanthus*, *Hemandradenia*, *Jollydora*, *Schellenbergia*, and certain species of *Cnestis* and *Connarus* are trees. Trees belonging to *Jollydora* are palm-like in habit. Most other genera are erect shrubs, climbers, or lianes. The following description of the stem and leaf structure is largely based on that by Schellenberg (2029). The **hairs** include the following types. (i) Unicellular with one or two arms. (ii) Sympodial, branched hairs. (iii) Tufted. Glandular hairs are mostly confined to the floral organs. The **epidermis** consists partly or wholly of mucilaginous cells in several genera. **Stomata** are confined to the lower surface of the leaf, but the arrangement of the adjacent cells is somewhat variable, thus enabling certain groups of genera to be distinguished from one another (see 'Leaf'). **Secretory cells** and **cavities** of various types have been reported from the leaf and axis of certain members of the family. The **cork** arises superficially and the **pericycle** contains a composite and continuous ring of sclerenchyma in the few species which have been examined. The **phloem** of the axis contains **tannin-sacs** in *Connarus*. **Crystals**, where present, are stated to be exclusively solitary, and prismatic or pyramidal in shape.

(ii) Wood

Vessels medium-sized to large, almost exclusively solitary or with numerous multiples, occasionally with spiral thickening, perforations simple, intervascular pitting alternate, pits to parenchyma typically large and simple; members of medium length. **Parenchyma** typically absent or as a few cells round the vessels, sometimes in long crystalliferous strands among the fibres.

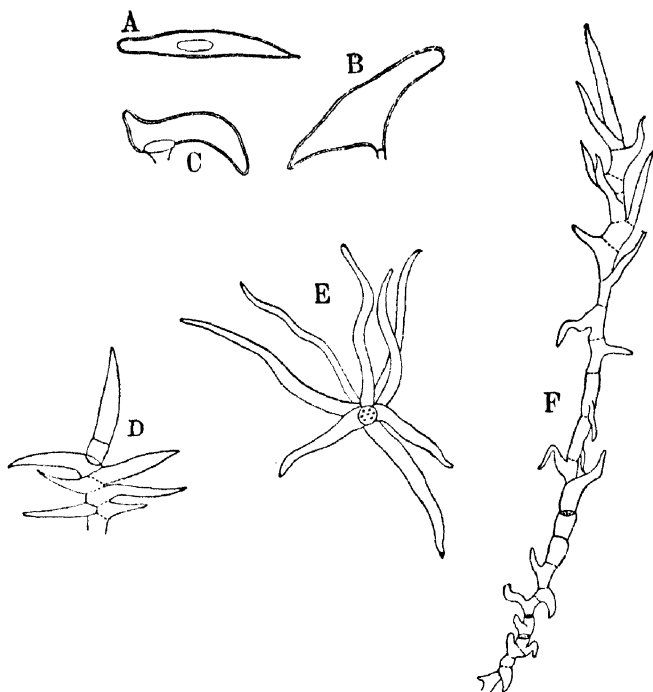


FIG. 105. *CONNARACEAE*

A-C, Two-armed and one-armed trichomes of *Connarus blanchetii* Planch. D-F, Branched hairs of species of *Connarus*: D-E, *Connarus fulvus* Planch.; F, *Connarus pachyneurus* Radlk.; the trichome in E is seen from above, that in D and F from the side.—By Solereder.

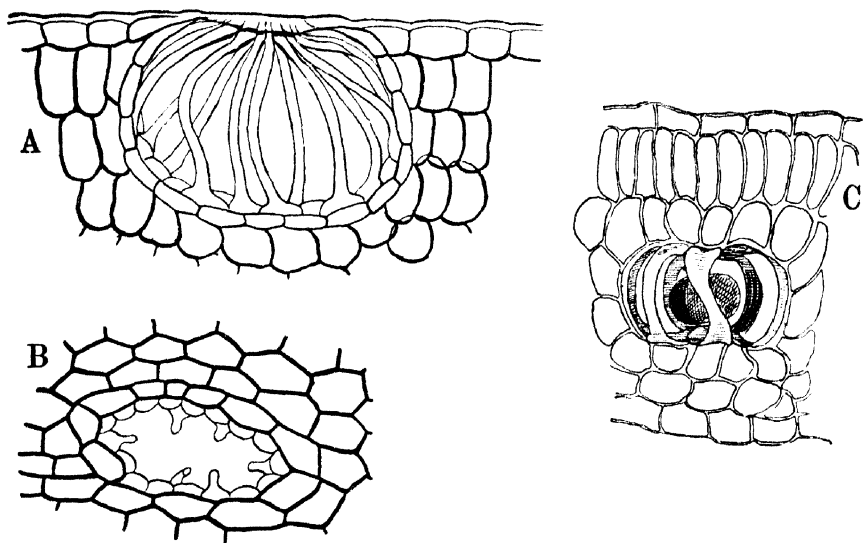


FIG. 106. *LEGUMINOSAE—PAPILIONACEAE*

A, Transverse section through an intramural gland of the leaf in *Psoralea hirta* L. B, Transverse section through a secretory cavity in the primary cortex of *Lonchocarpus spruceanus* Benth., characterized by the papillose differentiation of the epithelium. C, Peculiar secretory cavity of *Lonchocarpus spruceanus* with bracket-epithelium.—By Solereder.

Rays exclusively uniseriate or occasionally biseriate, very numerous, composed entirely of upright cells, or of procumbent cells; or of both. **Fibres** with simple pits, septate, occasionally crystalliferous; moderately long; thin-walled groups often present, with a parenchyma-like distribution. **Vasicentric tracheids, latex tubes, gum cysts, and intercellular canals** present in some species. **Included phloem** of the 'concentric' type present in *Rourea*.

LEAF

Dorsiventral. **Hairs** (Fig. 105 A-F) mostly unicellular or occasionally bicellular, but exhibiting a considerable diversity of external form. Unicellular, 2-armed in *Connarus* and *Vismianthus*. Horizontal hairs supported by short pedestals recorded in *Bernardinia*, *Burttia*, and most species of *Connarus*. Hairs of *Jollydora* similar but multicellular. Sympodially branched, tree-like hairs, often appearing stellate when viewed from above, recorded in many species of *Connarus*. Stellate hairs, consisting of clusters of 4 or occasionally more members, also occur in *Agelaea*. Short, pin-like trichomes present amongst longer ones in *Manotes* (accompanied by glandular hairs in this genus), *Paxia* (forming a golden-yellow clay-like coating on young leaves and stems of *P. calophylla* Gilg), *Roureopsis*, *Spiropetalum*. Glandular hairs, mostly confined to the floral organs, recorded in *Cnestis*, *Connarus*, *Jollydora* (sometimes with long stalks, and resembling those of tobacco), *Pseudoconnarus*, *Rourea* (pro parte). **Epidermis** papillose on the lower surface in species of *Byrsocarpus*, *Cnestis*, *Pseudoconnarus* (very numerous), *Santaloides*; including a varying proportion of mucilaginous cells, which are frequently large and penetrate into the mesophyll, in species of *Bernardinia*, *Byrsocarpus*, *Castanola*, *Cnestis*, *Rourea*; mucilaginous cells typically absent from *Agelaea*, *Ellipanthus*, *Hemandradenia*, *Jollydora*, *Pseudellipanthus*, and usually lacking in *Connarus*. Epidermis appearing to consist partly or wholly of several layers owing to the formation of secondary divisions in species of *Byrsocarpus*, *Castanola*, *Cnestidium*, *Jaundeia*, *Paxia*, *Roureopsis*, *Santaloides*, *Spiropetalum*. Epidermal cells with vertical divisions recorded in *Paxia*, *Roureopsis*, *Spiropetalum*. **Stomata** confined to the lower surface, except rarely on the upper side in species of *Connarus*. Arrangement of the neighbouring cells very variable. Stomata rubiaceous in *Bernardinia*, *Byrsocarpus*, *Cnestis*, *Jaundeia*, *Jollydora*, *Paxia*, *Rourea*, *Roureopsis*, *Santaloides*, *Spiropetalum*, *Taeniochlaena*; surrounded by a circle of small cells in *Cnestidium*, *Connarus*, *Ellipanthus*, *Hemandradenia*, *Manotes*, *Pseudellipanthus*, *Pseudoconnarus*. Subsidiary cells in the first of these 2 groups of genera sometimes become subdivided, after which the stomata in both groups of genera resemble one another. Stomata caryophyllaceous in *Jollydora*; surrounded by 3 subsidiary cells in *Agelaea* and *Castanola*. For ecological specializations and other details of stomata see Schellenberg (2029). A **hypoderm** of thickened cells recorded beneath the upper epidermis in *Agelaea oligantha* Gilg (locally) and *Connarus* spp. **Mesophyll** not usually exhibiting any special characters; palisade tissue consisting of cubical cells in species of *Jollydora*. Solitary stone cells frequent in the mesophyll above and below the midrib in most genera. Sclerosed elements also recorded on the inside of the lower epidermis in *Rourea ligulata* Baker. Secretory cavities recorded in *Castanola*, *Connarus*, *Vismianthus*; those of *Castanola* consisting of spaces filled with mucilage in

the spongy tissue, and, in *Connarus* and *Vismianthus*, of cavities filled with brown resinous material in all parenchymatous tissues. Vascular bundles of the **veins** usually accompanied by sclerenchyma, frequently extending from the vascular bundle to the upper surface of the leaflet. Bundles less frequently surrounded by ordinary mesophyll cells, but this occurs in *Jollydora* and *Pseudconnarus* and also in certain species of *Paxia*, *Roureopsis*, *Santaloides*, *Spiropetalum*, *Taenochlaena*. Small cells, each containing a solitary **crystal**, present above and below the bundles, especially in the *Eucnestis* section of *Cnestis* (but not in the sub-genus *Ceratocnestis*) and in *Manotes*. Solitary crystals only have been recorded in the family, notably in species of *Agelaea* and *Cnestis*. Small crystals also stated to occur in the mucilaginous lining of the epidermal cells in certain species of *Rourea*. **Secretory cavities**, see 'Mesophyll'. For anatomy of the leaf joint (pulvinus) see Sperlich (2167) and Funke (734).

AXIS

YOUNG STEM

Cork arising in the sub-epidermis in species of *Connarus* and *Rourea*, composed of cells with fairly wide lumina. Primary **cortex** containing mucilage cavities formed from cells with mucilaginous membranes in *Rourea induta* Planch. **Pericycle** containing a composite continuous ring of sclerenchyma in species of *Connarus* and *Rourea*. Secondary **phloem** including tangential groups of tannin sacs with wide lumina in *Connarus fulvus* Planch.; provided with groups of fibres in *Rourea induta*. **Xylem** in the form of a continuous cylinder traversed by narrow rays; vessels with simple perforations. **Crystals** said to be exclusively solitary.

WOOD (Fig. 104 c and f)

Vessels large (mean tangential diameter more than 200 μ) in *Byrsocarpus*, *Connarus*, and *Manotes*, medium-sized in some specimens of these and in the other genera; sometimes nearly all solitary, particularly where the vessels are of the liane type, but otherwise commonly with numerous radial multiples, which are sometimes of 4 or more cells in *Connarus* and produce a radial pattern in *Byrsocarpus*; in addition there may be long clusters of 1-3 rows of small angular vessels in *Cnestidium* and *Connarus* (938); mostly 7-15 per sq. mm.; semi-ring-porous in some species of *Connarus*; spiral thickening reported, at any rate in the smaller vessels or at the tips of the members, in *Connarus* (938, 1868) and *Ellipanthus* (1154). Perforations simple. Intervascular pitting alternate, moderately small to moderately large; Heimsch (938) states that some opposite pit-pairs are present in all species; pits to wood and ray parenchyma mostly large and simple, varying from round to horizontally elongated and sometimes slightly angular. Solid deposits and tyloses present in some specimens, the tyloses sclerosed in *Byrsocarpus*. Mean member length 0.5-0.7 mm. **Parenchyma** typically scanty paratracheal, e.g. in *Ellipanthus*, or absent. Williams (2430) describes the parenchyma of *Connarus* as 'metatracheal; in widely and irregularly spaced concentric lines or bands', but this is not typical of the material examined by the author. With long, fibre-like strands of chambered crystals scattered among the fibres in all the genera except *Byrsocarpus* and *Rourea* (938). **Rays**

exclusively uniseriate or with a few biseriata in addition, though Solereder records rays up to 5 cells wide in *Cnestidium lasiocarpum* Bak.; about 19 per mm.; the type of cell varying from square or upright only, e.g. in some species of *Connarus* and *Rourea* (Kribs's Heterogeneous Type III), to procumbent only, e.g. *Ellipanthus* (Kribs's Homogeneous Type III); frequently filled with gummy contents; in echelon in *Ellipanthus*. **Fibres** with simple pits, equally numerous on both radial and tangential walls; septate; usually with moderately thin walls. Often with groups of thinner-walled fibres, which also differ in contents, that in transverse sections resemble bands or patches of parenchyma. According to Janssonius these cells in *Ellipanthus* are distinctly shorter than the other fibres. Crystalliferous, with the crystals separated by septa, in *Cnestidium* (938) and *Connarus*. Mean length 0.7–1.0 mm. **Vasicentric tracheids** present in, at least, some species of *Byrsocarpus*, *Cnestidium* (938), *Connarus*, *Manotes*, and *Rourea*; usually intermediate in length between the vessel members and the fibres and straight to irregular in shape; sometimes with spiral thickening (938). Structures resembling **latex tubes** are described by Heimsch (938) in the rays of *Connarus* and also reported by Record and Hess (1886) for *Cnestidium*. **Intercellular canals** of the vertical type noted by Heimsch (938) in *Connarus martii* Schellenb.; Heimsch also records the occurrence of scattered secretory cavities, which may be cyst-like or elongated vertically, in other species of *Connarus* and in two species of *Cnestidium*. **Included (interxylary) phloem** of the 'concentric' type (*c.l. circumvallatum*) present in *Rourea pulchella* Planch., with successive layers of xylem and phloem separated by broad bands of conjunctive tissue containing numerous layers of stone cells.

TAXONOMIC AND PHYLOGENETIC NOTES

Schellenberg (2029) has discussed the possible relationships between the Connaraceae and other families, and also the phylogenetic relationships between the genera within the Connaraceae. Anatomical features are not taken into consideration to any great extent in the discussion.

Heimsch (938) considers that the wood of the Connaraceae is structurally of an advanced type and similar to most other families of the Sapindales, though he points out that the evidence of the wood structure alone cannot decide whether this indicates a true relationship or merely parallel development. He suggests that the Connaraceae may belong to Hutchinson's 'Pinnatae', standing near the Sapindaceae rather than the Rosaceae or Leguminosae.

ECONOMIC USES

The family does not yield many economic products. *Connarus africanus* Lam. is stated to possess anthelmintic properties, while the seeds of species of *Bernardinia*, *Byrsocarpus*, *Cnestis*, *Connarus*, *Rourea* have been used locally as poisons. The fruit of *Cnestis natalensis* (Hochst.) Planch. et Sonder is edible, and known locally as wild pear.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Agelaea, Bernardinia, Burtia, Byrsocarpus, Castanola, Cnestidium, Cnestis,

Connarus, Ellipanthus, Hemandradenia, Jaundea, Jollydora, Manotes, Paxia, Pseudellipanthus, Pseudoconnarus, Rourea, Roureopsis, Santaloides, Spiropetalum, Taeniochlaena.

(ii) FOR WOOD STRUCTURE

Byrsocarpus, (Cnestidium), (Cnestis), Connarus, Ellipanthus, (Jollydora), Manotes, Rourea.

LITERATURE

(i) *On General Anatomy*

Courchet 485, Funke 734, Schellenberg 2027, 2028, 2029, Sperlich 2167.

(ii) *On Wood Structure*

Heimsch 938, Janssonius 1154, Record 1843, 1851, 1864-72, Record and Hess 1886, Stone 2202, 2207, Williams 2430.

115. LEGUMINOSAE

115 A. MIMOSACEAE

(FIG. 107 on p. 478; FIG. 108 on p. 482; FIG. 118 on p. 536)

SUMMARY

(i) GENERAL

A tropical and sub-tropical family, consisting mostly of trees and shrubs, but including lianes and a few herbs. The leaves of certain members of the family exhibit 'sensitive movements'. Distinctive features are not numerous. Both glandular and non-glandular **hairs** of various types occur, the former being universally present. Uniseriate hairs, each consisting of short basal cells and an elongated distal cell, which are common amongst the Papilionaceae, have not been recorded in the Mimosaceae. Two-armed hairs, which occur in certain genera of Papilionaceae and Caesalpiniaceae, also appear to be absent. **Glands** occur on the petioles of most members of the family. The **epidermis** of the leaf is papillose or sub-papillose in a considerable number of genera. Vertical and horizontal divisions of the epidermal cells have been recorded in a few instances, but true hypoderm is unknown. The **stomata**, in nearly all recorded instances, are rubiaceous. The structure of the **mesophyll** varies considerably according to the type of leaf; the larger pinnules being dorsiventral and the smaller ones centric. The centre of the mesophyll in a number of genera contains relatively little chlorophyll, the cells being filled with brown tanniniferous contents. Fibres, connected to the sclerenchyma of the veins, also occur in the mesophyll of some species. The **crystals** are usually solitary rhombohedra, rod-shaped, and sometimes resemble styloids. When present in the axis they are generally situated in chambered fibres. **Secretory elements**. Cells with variously coloured contents occur in the leaf of a number of genera. Elongated secretory sacs have also been recorded in the leaf in a few instances, but they are much more common in, and characteristic of, the soft phloem of the young stem. **Tannin** is very common in the tissues in all parts of the plant. Its occurrence, distribution, and possible function have been discussed by Byl (326) with special reference to *Acacia*. Phyllodes are common, and in these the vascular bundles are arranged in a ring which, in most instances, is compressed so as to conform to the flattened shape of the phyllode. According to Shirley and Lambert

(2091) they usually bear stomata in equal numbers on both surfaces. For details concerning the structure of the phyllodes of *Acacia* see the articles by Buscalioni and Catalano (318, 319), Wood (2458), Peters, P. (1702), Peters, T. (1703), and Boke (217). The assimilatory stems of the long-rooted, umbrella-shaped acacias such as *A. seyal* Del., which grow in regions of restricted rainfall, are also noteworthy on account of their specialized anatomical structure. (For further details see 'Young Stem'.) Transverse sections through the distal end of the **petiole** in the small number of species which have been investigated exhibit a continuous or interrupted ring of bundles, accompanied by a few lateral ones. In the young stem the **cork** arises superficially in the few species investigated. **Aerenchyma** is sometimes developed instead of cork in *Mimosa cinerea* Vell. and *Neptunia oleracea* Lour. The **pericycle** is generally characterized by a composite and continuous ring of sclerenchyma. Centric **medullary bundles** have been recorded in *Elephantorrhiza burchellii* Benth. **Winged** and **grooved stems** occur in some, but by no means all, of the lianes in this family, whilst true **anomalous structure** occurs in *Entada*, where strands of sieve tubes develop in the parenchymatous groundwork of the xylem. The well-known **gum** of the Acacias is formed from parenchymatous elements in the pericycle, phloem, and wood.

(ii) Wood

Vessels typically mostly solitary but with a few small multiples and irregular clusters; with a rather vague oblique or tangential pattern in some species; ring-porous or semi-ring-porous in a few species; perforations simple, intervacular pitting alternate and small, pits to parenchyma similar; pits vested; members of medium length to very short. **Parenchyma** usually abundant, typically paratracheal, in round or diamond-shaped sheaths, and commonly also with diffuse strands which usually contain 11 or more chambered crystals; paratracheal parenchyma occasionally confluent or in regular broad bands; terminal bands present in many species but seldom conspicuous; chambered crystals common in both the diffuse and the paratracheal parenchyma; strands usually of 2-4 cells, fusiform parenchyma cells common in some species. **Rays** 1-9 (mostly 2-5) cells wide or exclusively uniseriate; cells typically narrow tangentially; homogeneous with few uniseriates in about two-thirds of the genera with multiseriate rays; with some tendency to echelon or storied arrangement in all species, but seldom distinctly storied. **Fibres** with small, simple pits; septate in some genera; moderately long to moderately short. **Intercellular canals**, of the vertical traumatic type, very rare.

LEAF

Dorsiventral, isobilateral or centric. **Hairs** including both glandular and non-glandular types. Two-armed and uniseriate hairs consisting of short basal cells accompanied by an elongated distal cell not common, but hairs consisting of an elongated cell and 2 basal cells sunk in the epidermis recorded by Kienholz (1236) in *Sophora tomentosa* Linn.

I. Non-glandular hairs

- (a) Unicellular or uniseriate, in the latter case with thin division walls.
 - (i) Uniseriate but with a bulbous base in *Albizzia* sp. (ii) Unicellular,

one-armed, but with a swelling in the place where a second arm might be expected in *Inga* and *Xylia*. (iii) Unicellular, bracket-shaped, hooked in species of *Calliandra*. (iv) With the base surrounded by a rosette of cells having cystolith-like thickenings in *Affonsea juglandifolia* St. Hil.

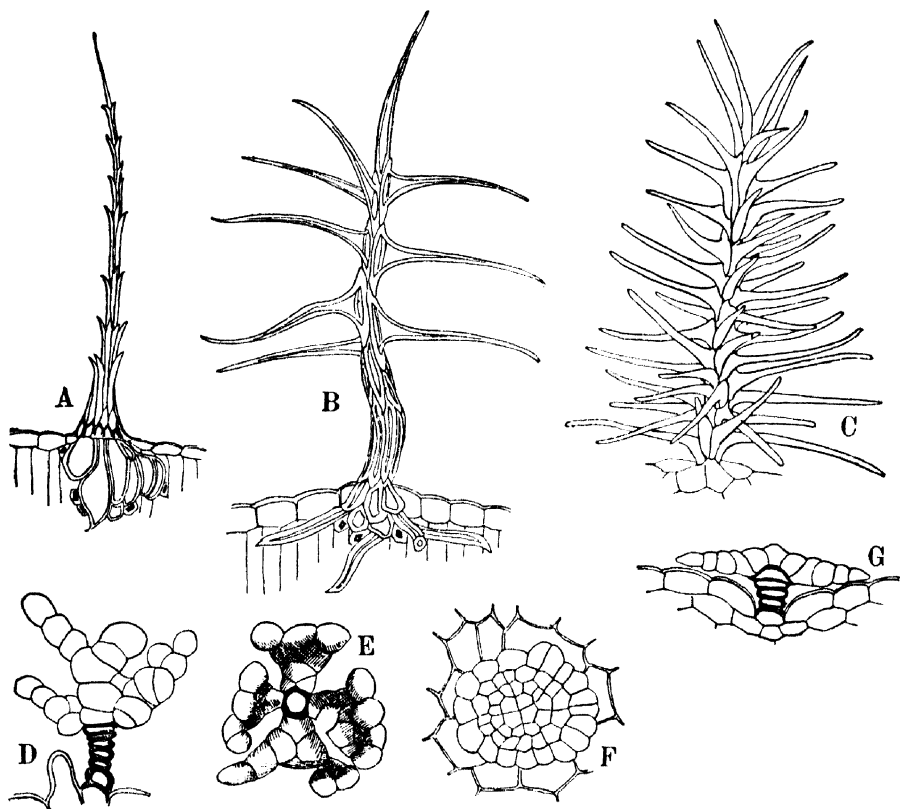


FIG. 107. LEGUMINOSAE

A, Shaggy hair of *Mimosa obtusifolia* Willd. B, Shaggy hair of *Mimosa furfuracea* Benth., resembling a fir-tree. To the base of both of these sclerenchymatous cells are attached, which, penetrating into the mesophyll, anchor the hair firmly, and are accompanied by crystal-cells (crystals shaded). C, Shaggy hair of *Mimosa incana* Benth., resembling a fir-tree. D-E, Branched glandular hairs of *Mimosa spruceana* Benth.; E, Gland seen from above. F-G, Peltate gland of *Mimosa punctulata* Spruce.—By Solereder.

- (b) Branched shaggy hairs (Fig. 107 A-C) of various types in numerous species of *Mimosa*, possibly of specific diagnostic value.
- (c) Tufted hairs recorded in species of *Pentaclethra* and *Prosopis*.

II. Glandular hairs

- (a) Hairs with uniseriate stalks and ellipsoidal, multicellular heads of variable size recorded in species of *Acacia*, *Adenantha*, *Affonsea*, *Albizzia*, *Calliandra*, *Desmanthus*, *Elephantorrhiza*, *Entada*, *Enterolobium*, *Gagnebina*, *Inga*, *Leucaena*, *Lysiloma*, *Mimosa*, *Neptunia*, *Parkia*, *Pipta-*

denia, *Pithecolobium*, *Prosopis*, *Schrankia*, *Serianthes*, *Stryphnodendron*, *Xylia*.

- (b) Peltate, with heads of various sizes in species of *Acacia* and *Mimosa* (Fig 107 F-G).
- (c) Branched or palmately divided glandular hairs present on the lower side of the leaf in *Mimosa spruceana* Benth. (Fig. 107 D-E).
- (d) Glandular shaggy hairs with multi- or uni-seriate stalks and spherical or obconical heads in a number of species of *Mimosa*.

Glands, consisting of groups of parenchyma cells situated above bundle-endings and surrounded by abundant crystals, present in the petiole of most members of the family. The occurrence and distribution of glands in Australian Acacias have been described by Hardy (889). They are to be found on the upper edge of the petiole, rachis, or phyllode, and are most numerous in the Bipinnatae, where there is usually a gland situated immediately below the base of each pair of pinnae. In the Phyllodineae they occur relatively high up (towards the distal end) in species with relatively broad phyllodes, but more towards or below the base in species with long phyllodes. Certain species belonging to the same group bear 2 or more glands, and several have an auxiliary nerve connecting the marginal gland obliquely to the midrib, but this inconstant feature is said to be restricted to the Uninerves. Glands are absent from or most inconspicuous in members of the Calamiformes and other Acacias from the dry north-west districts of Victoria. **Cuticle** usually verrucose or granular, rarely smooth. Leaf surface sometimes covered with a white deposit of a wax-like substance in species of *Acacia* and *Mimosa* or by a resinous secretion from glandular hairs in *Acacia* sp.; sometimes having a varnished appearance owing to the structure of the cuticle itself in species of *Mimosa*. **Epidermis** with short, hemispherical papillae on the lower side of the leaf in species of *Acacia*, *Calliandra*, *Enterolobium*, *Mimosa*, *Pithecolobium*, *Sophora*, *Stryphnodendron*, with mammiform papillae in *Albizzia*, *Enterolobium*, *Mimosa*, *Pithecolobium*, occasionally with finger-shaped papillae in *Albizzia* and *Pithecolobium*. Epidermis sub-papillose, particularly on the lower surface, in species of *Adenanthera*, *Albizzia*, *Calliandra*, *Elephantorrhiza*, *Entada*, *Enterolobium*, *Gagnebina*, *Leucaena*, *Lysiloma*, *Piptadenia*, *Pithecolobium*, *Plathymenia*, *Prosopis*, *Serianthes*, *Stryphnodendron*. Outer walls of the epidermal cells often considerably thickened; with ridge-like external projections either on the whole surface, or confined to the region of the stomata, in species of *Acacia* and *Mimosa*. Inner walls of the epidermal cells frequently mucilaginous in species of *Acacia*, *Adenanthera*, *Albizzia*, *Calliandra*, *Desmanthus*, *Dichrostachys*, *Elephantorrhiza*, *Entada*, *Leucaena*, *Lysiloma*, *Mimosa*, *Neptunia*, *Parkia*, *Piptadenia*, *Pithecolobium*, *Schrankia*, *Serianthes*, *Stryphnodendron*. Epidermal and adjacent cells silicified in species of *Calliandra* and *Pithecolobium*. Epidermal cells usually with vertical divisions in *Enterolobium*; with vertical and horizontal divisions in *Albizzia ferruginea* Benth. **Hypoderm** not recorded. **Stomata** often confined to the lower surface, particularly amongst the Adenanthereae, Ingeae, and Parkieae; uniformly distributed on both sides of the leaf in the Acacieae, the Eumimoseae, as well as in *Dichrostachys* and *Neptunia*; confined on the lower side to the bases and on the upper side to the tips of the leaflets in a few species of

Mimosa and *Piptadenia*, this peculiar distribution possibly being correlated with the 'sleep-position' assumed by the leaflets. In *Mimosa cruenta* Benth. stomata occur all over the upper surface, but on the lower side they are confined to one longitudinal half of each leaflet. They are absent altogether from the lower side of the basal leaflet. These features correspond with the 'sleep-position' of the leaves of the species in question, the parts of the epidermis which bear stomata being covered, while the parts free from stomata are not covered during 'sleep'. Stomata usually rubiaceous except where this is obscured by transverse or oblique secondary division of the subsidiary cells, e.g. in species of *Acacia* and *Pithecolobium*. **Mesophyll** structure varying according to the size and shape of the leaflets; dorsiventral in the large pinnules of *Inga*; centric in small, narrow leaflets; with 3–4 layers of palisade cells on the adaxial side and of arm-palisade cells on the abaxial side in *Acacia senegal* Willd. according to Sabnis (1977). The vertical phyllodes of *Acacia* are also centric. Central portion of the mesophyll often differentiated from the remainder by being relatively free from chlorophyll, the cells instead often containing brown tanniniferous materials in species of *Acacia*, *Calliandra*, *Elephantorrhiza*, *Leucaena*, *Lysiloma*, *Mimosa*, *Pithecolobium*, *Prosopis*. Groups of water-storage cells present in the mesophyll of *Sophora tomentosa* L. Fibres connected with the sclerenchyma of the veins, but much more abundantly developed in some species than in others, recorded in the mesophyll of *Affonsea*, *Calliandra*, *Inga*, *Parkia*, *Pithecolobium*. Spool-shaped stone cells recorded by Kienholz (1936) below the upper and lower epidermis in *Prosopis* sp. Smaller **veins** usually embedded in the mesophyll, but accompanied and generally surrounded by sclerenchyma; vertically transcurrent by thin-walled tissue in species of *Calliandra*, *Plathymenia*, *Xylia*, and by sclerenchymatous tissue in *Stryphnodendron coriaceum* Benth. Many of the veins said by Kienholz (1936) to be sheathed by colourless parenchymatous cells in *Prosopis* sp. Enlarged terminal tracheids occur in *Adenanthera* and *Piptadenia*. Vascular bundles of the phyllodes arranged in a ring, compressed to correspond with the flattening of the petiole, the xylems of the opposed pairs of bundles being directed towards one another, and the phloem groups of each connected to the epidermis by a small mass of sclerenchyma. **Petiole** in transverse sections through the distal end, exhibiting a continuous or interrupted ring of bundles, accompanied by accessory bundles in the wings in species of *Acacia* (Fig. 118 A), *Entada*, *Inga* (Fig. 118 C), *Mimosa*, *Pithecolobium*. Main vascular strand dorsally flattened in *Pithecolobium dulce* Benth.; consisting of a ventral arc and a separate dorsal portion in '*Prosopis jacari* Hort.' (Fig. 118 B). A large accessory, centric, medullary bundle with central phloem observed in *Inga punctata* Willd. Main vascular strand of the petiole supported by 'pericyclic' fibres in all of the species examined at Kew. Further details concerning petiole structure have been recorded by Morvillez (1960) and Watari (2364). **Crystals** predominantly solitary, often rhombohedral, less frequently resembling styloids; clusters recorded only in the mesophyll and accompanying the veins in *Mimosa* and *Piptadenia*. Crystals in many species particularly numerous below the bases of the hairs. Some of the mesophyll cells not infrequently divided into chambers, each containing one crystal embedded in a local thickening of the cell wall.

Secretory elements.

I. *Cells*. (a) With colourless contents, in the spongy parenchyma, and appearing as transparent dots recorded in certain species of *Calliandra*, *Pentaclethra*, *Pithecolobium*, *Prosopis*. (b) With colourless or yellow contents, and arranged in groups in the neighbourhood of the veins in species of *Pentaclethra* and *Pithecolobium*. (c) Tubular or rounded, with yellowish contents and mucilaginous walls, occurring in all parts of the mesophyll in certain species of *Prosopis* belonging to the section *Algaroba*. (d) With undetermined contents, observed in the unligified tissues of the phloem in species of *Acacia*, *Inga*, *Mimosa*, *Pithecolobium*, examined at Kew.

II. *Sacs*. Recorded in species of *Pithecolobium*, and probably occurring elsewhere as well.

The anatomy of the leaves of members of the family which exhibit 'sensitive movements' has been studied by Steckbeck (2190) and Funke (734). Steckbeck concluded that the movements are controlled by crystals in the endodermis, each of which is surrounded by a protoplasmic sac and provided with intercellular protoplasmic connexions.

AXIS**YOUNG STEM (Fig. 118 D-E)**

Cork arising superficially in all recorded instances; sometimes in the second or third layer of cells below the epidermis; more rarely in the sub-epidermis. Evidence of occasional deep-seated cork reported for *Acacia* (see 'Economic Uses'). Cork cells slightly flattened or almost cubical; occasionally sclerosed on one side in *Acacia*; thickened on all sides in *Inga*; sometimes with delicate walls. Cork in *Acacia armata* R. Br. consisting of an outer, crushed layer of tanniferous cells, a central region of very regular thin-walled cells without contents and an inner zone of irregular, densely tanniferous cells; crystals abundant in all parts of the cork. Cork replaced by **aerenchyma** on the bladder-like swellings of the stem of the floating plant *Neptunia oleracea* Lour., but normal cork is produced in the same position when more mature. Metcalfe (1494) confirmed that the aerenchyma originates from a phellogen in the outer part of the cortex and consists of cells with cellulose walls and living contents. Aerenchyma also recorded on the stems and peduncles of *Mimosa cinerea* Vell. Primary **cortex** consisting of thin-walled cells or of collenchyma, often containing tannin; composed of specially large cells in *Parkia filicoides* Welw. Stone cells recorded in the primary cortex only in *Albizzia anthelminthica* Brogn. **Pericycle** usually containing a continuous and frequently composite ring of sclerenchyma, the fibres often being mucilaginous or unligified; strands of fibres less common. Secondary **phloem** sometimes stratified into fibrous and soft portions. Distal ends of the rays, where traversing the phloem, frequently broadened towards the outside; generally devoid of sclerotic cells. Sieve tubes provided with scalariform sieve plates. **Xylem** in the form of a continuous cylinder traversed by narrow rays, more interrupted by broader rays in some genera. Vessels with simple perforations. **Pith** generally consisting of lignified cells except in aquatic species of *Desmanthus*, *Dichrostachys*, *Mimosa*, *Neptunia*. **Medullary bundles**, consisting of soft phloem surrounded by xylem almost devoid of vessels, recorded in *Elephanto-*

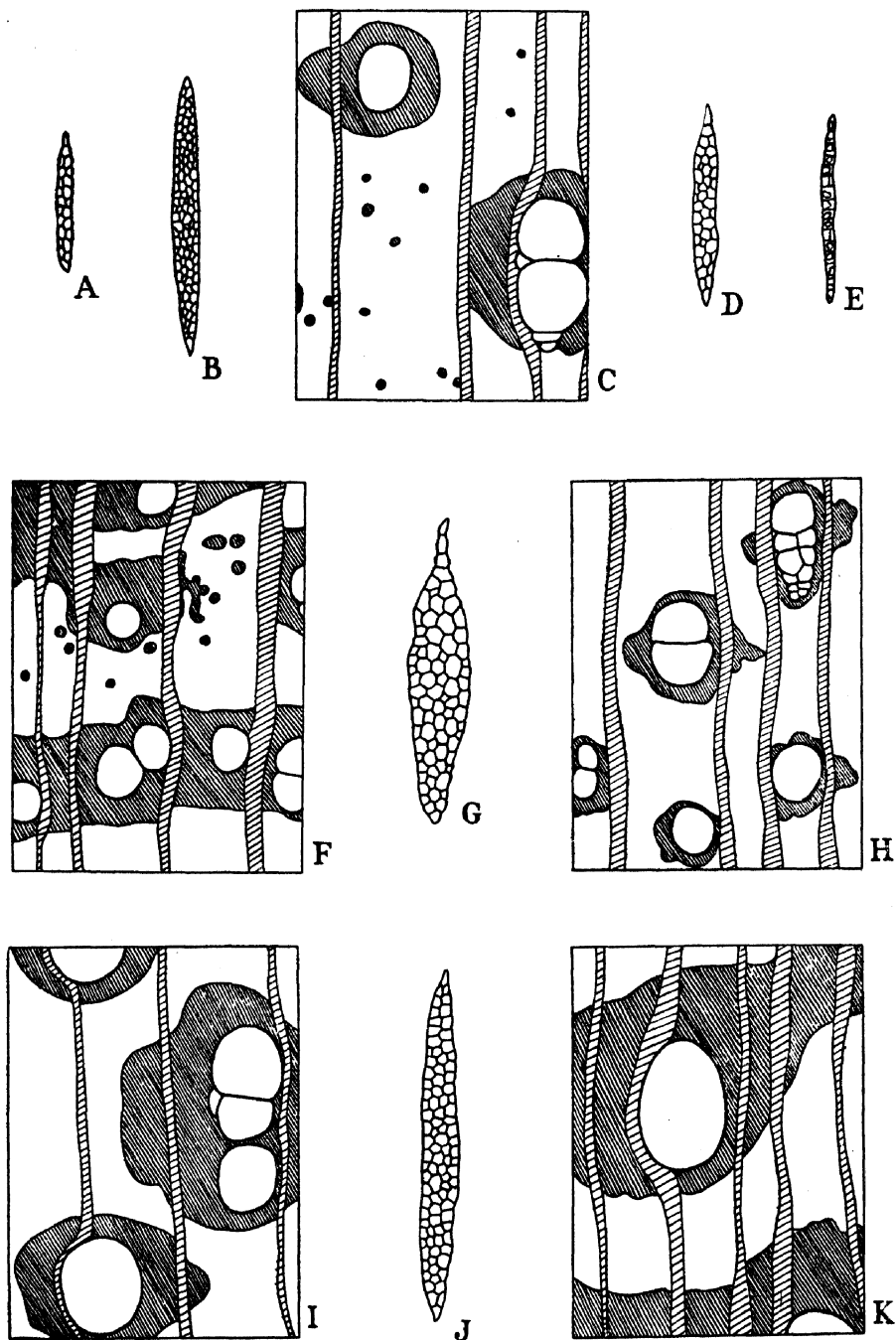


FIG. 108. LEGUMINOSAE—MIMOSACEAE

A, *Acacia melanoxylon* R. Br. B, *Piptadenia africana* Hook. f. C, *Albizzia odoratissima* Benth. D, *A. lucida* Benth. E, *Dichrostachys glomerata* Chiov. Crystalliferous parenchyma strand. F, *Vachellia astringens* Speg. G, *Entada abyssinica* Steud. H, *Acacia nilotica* Del. I, *Piptadenia africana* Hook. f. J, *Pithecolobium confertum* Benth. K, *Adinobotrys atropurpureus* Dum.

rhiza burchellii Benth. **Secretory elements.** Cells with undetermined but probably tanniniferous contents observed in the cortex of certain species of *Acacia*, *Inga*, *Mimosa*, and *Pithecolobium* represented in the Kew slide collection, in the phloem and medullary rays of the same genera and species except *Mimosa*, and in the pith of *Acacia* and *Inga*. Elongated secretory sacs, resembling the tanniniferous sacs of the Papilionaceae, but filled with various substances, also recorded by Solereder in *Mimosa*, their presence in other genera also being implied. For tanniniferous cells see also 'Cork' and 'Cortex'. Solitary **crystals** stated to occur in thickenings of the cell walls of the primary cortex and in chambered fibres in the phloem; large or very large solitary crystals observed in the cortex and phloem of several species. Groups of small crystal cells also recorded in the pith of species of *Adenanthera*, *Desmanthus*, *Dichrostachys*, and *Neptunia*. See also under 'Cork'. The **gum** of the acacias is said to be formed by the transformation of parenchymatous elements in the pericycle, phloem, and wood. Some details concerning the structure of young stems of Australian acacias have been published by Shirley and Lambert (2091).

Hagerup (866) has drawn attention to the interesting structure of the assimilatory stems of **umbrella-shaped acacias** such as *A. seyal* Del. These plants, with long tap-roots, grow in localities where water supplies are restricted except during a brief annual period of high rainfall. The green, primary cortex which is the chief assimilatory tissue, is protected by an external layer of cork consisting of living cells with translucent contents. Only the outermost layer of cork is composed of cells with thickened inner walls, and this layer becomes disorganized and cast off in the form of a red powder as the stem grows older. The next layer of cork cells then becomes thickened and behaves in the same way. Air diffusion occurs through numerous lenticels. Leaves are developed only during the wet season when they serve as accessory assimilatory organs. The outer layer of cells of the thorns is filled with air, and is thought to reflect the light on to the lateral assimilatory surfaces of the branches, which are also illuminated below by reflection from the brightly coloured ground. Hagerup points out that the plants are not unlike cacti during the unfavourable season, whilst the development of leaves during rainy periods makes them more like trees in a tropical rain forest.

WOOD (Fig. 108)

Vessels typically medium-sized (100–200 μ mean tangential diameter) to large; small in *Serianthes myriadenia* Planch. and *Vachellia* spp., largest in some species of *Adinobotrys*, *Albizzia*, *Entada*, *Enterolobium*, *Fillaeopsis*, *Parkia*, *Piptadenia*, and *Pithecolobium*; typically solitary with a few multiples of 2 or 3 cells and some irregular clusters; these clusters (Fig. 108 H), usually of small vessels, are not present in every section, but a tendency to produce them locally appears to be characteristic, particularly of *Acacia*, *Inga*, *Pentaclethra*, *Samanea*, *Tetrapleura*, and *Vachellia*; such clusters often accompanied or replaced by multiples of one large and several small vessels, e.g. in some species of *Acacia*, *Amblygonocarpus*, *Enterolobium*, and *Xylia*; with a tendency to an oblique pattern in some species, e.g. of *Albizzia* and *Calpocalyx*, *Pithecolobium* (1894) and in occasional tangential rows in some species of *Acacia*, *Albizzia* (1154), *Lysiloma*, *Parkia*, *Piptadenia* (2430), *Prosopis* (1894),

and *Vachellia*; mostly 1.5–5 per mm., rather more numerous (mostly between 5 and 10 per mm.) in some species of *Abarema*, *Acaciella*, *Cedrelinga*, *Chloroleucon*, *Cojoba*, *Dichrostachys*, *Faidherbia*, *Leucaena*, *PoPONax*, *Prosopis*, and *Vachellia*; semi-ring-porous in some species of *Acacia*, *Albizzia*, *Parkia*, *Prosopis* (1894), and *Vachellia*, sometimes with a distinct zone at the beginning or end of the growth ring, of vessels that are smaller than those of the rest of the ring; spiral thickening reported by Record (1864) in *Prosopis*. Perforations simple. Intervascular pitting alternate, small; very small in *Abarema*, *Calliandra*, *Cojoba*, *Lysiloma*, and *Wallaceodendron*, only moderately small in *Enterolobium*, *Parkia*, and *Plathymenia*; sometimes with coalescent apertures; pits to parenchyma similar to the intervacular pitting; vested. Solid deposits present in most of the species; tyloses not observed. Mean member length usually 0.2–0.4 mm. Greiss (816, 817) has investigated the effect of different conditions of water-supply on the structure of the wood of *Acacia arabica* var. *nilotica* Forst. and the effect of such changes of structure on the conductivity of the wood. **Parenchyma** usually abundant, and predominantly paratracheal, sometimes very abundant and occupying more space than the fibres, e.g. in *Entada* and *Faidherbia*; typically as a sheath, several cells wide, about the vessels, round, diamond shaped or distinctly aliform on cross-section and becoming confluent locally where the vessels are close together; with considerable variation within these limits in different parts of the ring and in different specimens; more consistently rounded (vasicentric) in some species of *Abarema*, *Acacia*, *Acaciella*, *Albizzia*, *Cedrelinga*, *Chloroleucon*, *Dichrostachys*, *Enterolobium*, *Inga*, *Piptadenia*, *Plathymenia*, *Prosopis*, and *Pseudosamanea*; more consistently confluent in some species of *Acacia*, *Adinobotrys* (Fig. 108 K), *Amblygonocarpus*, *Aubrevillea*, *Enterolobium*, *Parkia*, *Prosopis*, and *Vachellia* (Fig. 108 F); in broad bands (4-seriate or more) in *Acacia albida* Del., *Acacia farnesiana* Willd., *Adinobotrys*, *Calliandra*, *Entada*, *Faidherbia*, and *PoPONax*; scattered strands (diffuse), usually containing chambered crystals, present in *Acacia* (a few species only), *Adenanthera*, *Adinobotrys*, *Albizzia* p.p. (Fig. 108 c), *Calpocalyx* p.p., *Cathormion*, *Cedrelinga*, *Chloroleucon*, *Cojoba*, *Cylicodiscus*, *Dichrostachys*, *Inga*, *Leucaena*, *Lysiloma*, *Parkia*, *Piptadenia*, *Pithecolobium* p.p., *PoPONax*, *Pseudosamanea*, *Serianthes*, *Vachellia*, *Wallaceodendron*, and *Xylia*; sometimes with terminal parenchyma, e.g. in *Acacia* p.p., *Albizzia* p.p., *Amblygonocarpus*, *Calliandra*, *Fillaeopsis*, *Parkia*, *Pentaclethra*, *Vachellia*, and *Xylia*. Chambered crystals present in (a) scattered strands, in the genera listed above, and (b) in the paratracheal parenchyma, particularly on the margins, of nearly all the species examined, rare or absent from *Abarema*, *Acaciella*, *Adenanthera pavonina* L., *Albizzia antunesiana* Harms., *Enterolobium* spp., *Plathymenia reticulata* Benth., *Pithecolobium* p.p., and *Serianthes myriadenia* Planch.; the maximum number of crystals per strand seldom fewer than 11 and often many more (Fig. 108 E); the majority of the crystals in *Vachellia* large and contained in thick-walled idioblasts; with the chambered strands often locally biseriate in *Wallaceodendron celebicum* Koord., and, less commonly, in *Serianthes myriadenia* (tangential section); cells sometimes containing gum-like deposits. Often with pronounced intercellular spaces. Strands most commonly of 2–4 cells, fusiform parenchyma cells common in some species of *Acacia*, *Albizzia*, *Dichrostachys*, *Leucaena*, *Pithecolobium montanum* Benth. (1154),

Prosopis, and *Samanea*. Sometimes with a tendency to storied arrangement, e.g. in *Plathymenia*. In *Plathymenia* the sheath of vasicentric parenchyma is narrow but this is in turn surrounded by a sheath of septate fibres that, owing to their wider lumina and thinner walls, are distinct from those of the ground tissue. **Rays** mostly 2 cells wide; exclusively uniseriate or with only a few biseriate rays in *Abarema*, *Acacia* p.p., *Cedrelinga*, *Chloroleucon*, *Cojoba*, *Faidherbia*, *Pithecolobium* p.p., *Pseudosamanea*, *Serianthes myriadenia* (Benth.) Planc., and *Wallaceodendron celebicum*; 4–7 cells wide in at least some species of *Acacia*, *Adinobotrys*, *Albizzia*, *Dichrostachys*, *Entada*, *Entadopsis*, *Inga*, *Parkia*, *Piptadenia*, *Pithecolobium*, *Prosopis*, and *Vachellia*; 8 cells wide in some species of *Acacia* and *Prosopis*; woods with multiseriate rays usually with very few or very low uniseriate rays, but uniseriate rays moderately abundant in some species in which the maximum width is 2 or 3 cells, e.g. *Calliandra guildingii* Benth., *Calpocalyx klainei* Pierre, *Enterolobium saman* Prain, *Leucaena*, *Parkia singularis* Miq., *Samanea saman* (Jacq.) Merrill, *Wallaceodendron celebicum*, and *Xylia dolabriformis* Benth., and more rarely in some woods with larger rays, e.g. *Adinobotrys atropurpureus* Dum. and *Albizzia odoratissima* Benth.; mostly from 4 to 8 rays per mm. but more numerous (up to 14 per mm.) in some of the woods with small rays; homogeneous (Kribs's Type II, sometimes I or III); Kanehira (1206) records heterogeneous rays in *Caesalpinia sappan* L.; cells usually small (about 10 μ) in tangential diameter (Fig. 108 B), but distinctly larger in *Amblygonocarpus*, *Calpocalyx*, *Entada*, *Fillaeopsis*, *Prosopis* p.p., and *Tetrapleura*; commonly containing gum-like deposits, crystals extremely rare. Almost always with some tendency to arrangement in echelon or stories unless the rays are commonly 2 or more times the height of the cambial initials; storying least marked in some species of *Acacia*, *Calpocalyx*, *Inga*, *Prosopis*, and *Vachellia* and most distinct in some species of *Adinobotrys*, *Parkia*, *Pithecolobium* (1894), and *Plathymenia*. **Fibres** with few, small, simple pits, more numerous on the radial than on the tangential walls. Septate in *Albizzia*, *Arthrosamanea*, *Calpocalyx*, *Cathormion*, *Dugandia* (1886), *Havardia* (1886), *Inga*, *Leucaena* (1206, 1886), *Pentaclethra*, *Piptadenia*, *Pithecolobium* p.p., *Plathymenia* (see also under 'Parenchyma'), *Senegalia* (1886), and *Xylia*. Walls usually moderately to very thick, but thin in some species of *Acacia* (exceptional), *Albizzia*, *Entada*, *Enterolobium*, *Lysiloma*, *Parkia*, *Samanea*, and *Serianthes*; Janssonius (1154) states that the fibres next the paratracheal parenchyma are usually thinner-walled than the others and have intercellular spaces, and suggests this feature as one means of distinguishing the Mimosaceae from the Caesalpinaceae; sometimes with a gelatinous inner layer and sometimes containing starch or gum-like contents. Mean length 0.8–1.75 mm. **Inter-cellular canals** of the vertical traumatic type observed in *Entada abyssinica* Steud. and reported (1886) in '*Senegalia glomerata*'. **Growth rings** and seasonal development of the wood have been investigated by Coster (481) in *Acacia*, *Adenanthera*, *Enterolobium*, *Leucaena*, and *Pithecolobium* and by Chowdhury in *Acacia* (414) and *Albizzia* (415).

ANOMALOUS STRUCTURE

Winged or grooved stems occur in some, but by no means all, of the lianes belonging to this family. True anomalous structure recorded only in species

of *Entada* with secondary strands of sieve tubes embedded in the soft parenchyma forming the groundwork of the xylem. A similar groundwork of parenchyma forms the greater part of the xylem in *Entadopsis*.

TAXONOMIC AND PHYLOGENETIC NOTES

See under Papilionaceae, p. 527.

ECONOMIC USES

Gum Arabic, now derived from *Acacia senegal* Willd., was formerly obtained from *A. nilotica* Del. and other species of *Acacia*. Edible products are less numerous than in the Papilionaceae, but the pods of the Honey Locust (*Prosopis juliflora* DC.) are used for food in the West Indies and Mexico. The family is well known as a source of tannin derived from various barks such as the Wattles (*Acacia* spp.) in Australia, South Africa, India, and the warm parts of America. The Australian material has a particularly good record for a high tannin content. The blackish-violet bark of the 'Black Wattle' (*Acacia decurrens* Willd.) is one of the most important kinds. The anatomy of Australian wattle barks has been studied by Welch, McGlynn, and Coombs (2409) who give the following particulars. Epidermis persisting for a long time, occurring even in barks of considerable thickness. Surface of the bark of some trees coated with a whitish deposit of wax. Cork usually arising superficially, but evidence of its deep-seated origin observed in some specimens; composed of flattened cells with moderately thick walls and brown contents. Periderm seldom more than 0.2 mm. thick. Cortical tissues bounded internally by a more or less complete ring of irregularly-shaped, thick-walled stone cells. Phloem including tangential bands of sieve tubes, which soon become disorganized, situated between rows of parenchymatous cells. Phloem also including groups of thick-walled fibres, up to 0.6 mm. in tangential diameter and 0.1 mm. wide, each group partly or wholly sheathed by a single row of short, thick-walled crystalliferous cells. Secondary phloem occasionally containing concentrically arranged pockets filled with gum. Medullary rays uniseriate or multiseriate, broadening considerably in the outer part of the bark. Tannin present chiefly in the outer part of the medullary rays, in the primary and secondary cortex and in the phloem parenchyma. Tannin content partly determined by the amount of fibre present in the phloem, a high fibre content being correlated with a low yield of tannin. For further details concerning the microscopy and properties of wattle barks see Wiesner (2423) and Bodenshtab (211). Brocardet (276) has described the microscopical structure and properties of a number of barks from Brazil which yield tannin. These are derived from species of *Acacia*, *Calliandra*, *Enterolobium*, *Inga*, *Pithecolobium*, and *Stryphnodendron* and known under variations of such local names as Angico, Barbatimao, Cambuy, Winhatico, Inga, and Jurema.

This family produces a considerable variety of timbers and, though few of them are of world-wide importance, some are moderately widely known and many others have considerable local importance. Among the best known are Australian Blackwood, *Acacia melanoxylon* R. Br., Kokko, or East Indian Walnut, *Albizia lebbek* Benth., and Pyinkado, *Xylia dolabriformis* Benth. Timbers that are in demand locally are also obtained from other species of

Acacia and *Albizzia* and from species of *Enterolobium*, *Lysiloma*, *Marmaroxylon*, *Piptadenia*, *Pithecolobium*, and *Prosopis*.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acacia, * *Adenanthera*, *Affonsea*, *Albizzia*, *Calliandra*, *Desmanthus*, *Dichrostachys*, *Elephantorrhiza*, *Entada*, * *Enterolobium*, *Gagnebina*, *Inga*, * *Leucaena*, *Lysiloma*, *Mimosa*, * *Neptunia*, *Parkia*, *Pentaclethra*, *Piptadenia*, *Pithecolobium*, * *Plathymenia*, *Prosopis*, * *Schrankia*, *Serianthes*, *Sophora*, *Styphnodendron*, *Xylia*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Abarema, *Acacia*, *Acaciella*, *Adenanthera*, *Adinobotrys*, *Albizzia*, *Amblygonocarpus*, *Calliandra*, *Calpocalyx*, *Cathormion*, *Cedrelinga*, *Chlorouleucon*, *Cojoba*, *Cylicodiscus*, *Dichrostachys*, *Entada*, *Entadopsis*, *Enterolobium*, *Fillaeopsis*, *Inga*, *Leucaena*, *Lysiloma*, *Mimosa*, *Parkia*, *Pentaclethra*, *Piptadenia*, *Pithecolobium*, *Plathymenia*, *Poponax*, *Prosopis*, *Pseudosamanea*, *Samanea*, *Serianthes*, *Tetrapleura*, *Vachellia*, *Wallaceodendron*, *Xylia*.

LITERATURE

(i) *On General Anatomy*

Bodenstab 211, Boke 217, Brocardet 276, Buscalioni and Catalano 318, 319, Byl 326, Funke 734, Hagerup 866, Hardy 889, Hart 910, Kienholz 1236, Metcalfe 1494, Morvillez 1560, Peters, P. 1702, Peters, T. 1703, Roncagliolo 1947, Sabnis 1977, Shirley and Lambert 2091, Steckbeck 2190, Watari 2364, Welch, McGlynn and Coombs 2409, Wiesner 2423, Wood 2458.

(ii) *On Wood Structure*

Bailey 73, 78, Baker 104, Becking *et al.* 164, Beekman 167, Benoist 170, den Berger 179, 182, 183, Besson 186, Brown, F. B. H. 282, Burgerstein 310, 312, Chalk *et al.* 363, 364, Chowdhury 411, 414, 415, Cooper and Record 461, Coster 481, Dadswell 525, Dixon 592, Foxworthy 705, Giordano 786, Greiss 816, 817, Hess 960, Hopkinson 1083, Howard 1088, Janssonius 1154, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, Louis and Fouarge 1392, Messeri 1493, Metcalfe 1497, Pearson and Brown 1679, Pfeiffer, J. Ph. 1713, Record 1780, 1787, 1825, 1831, 1843, Record and Hess 1886, Record and Mell 1894, Scott 2075, Stone 2202, 2206, 2207, Tang 2231, Williams 2430.

115 B. CAESALPINIACEAE

(FIG. 109 on p. 490; FIG. 110 on p. 494; FIG. 111 on p. 498; FIG. 118 on p. 536)

SUMMARY

(i) GENERAL

This mainly tropical family consists chiefly of trees and shrubs, and unlike the *Papilionaceae*, includes but few herbs. The glandular and non-glandular **hairs** are of various kinds, but the uniseriate type with short basal cells and an elongated distal cell, so common amongst the *Papilionaceae*, is rare. The **epidermis** is often papillose and sometimes mucilaginous. The arrangement of the subsidiary cells around the **stomata** is very variable, even within a single species, the 2 main types being the rubiaceous and ranunculaceous. This variability in the structure of the stomata is also a notable feature of the *Papilionaceae*. **Secretory elements.** Secretory cells, with varied contents,

are common in the mesophyll, but according to Solereder the tanniniferous idioblasts, which are so common in the Papilionaceae, are rare in the Caesalpinaceae. Tanniniferous cells were, however, found to be common in the cortex, phloem, and pith of young stems of various species grown at Kew (see 'Young Stem'). Secretory cavities, lined with epithelium, also occur in the leaf of certain genera, and are sometimes present in the primary cortex, pericycle, xylem, or pith of the axis as well. Secretory canals, which cannot easily be distinguished in transverse sections from elongated cavities, sometimes occur in the axis. The vascular bundles of the leaf **veins** are usually accompanied by sclerenchyma, and they are embedded in the mesophyll in some species, but vertically transcurrent in others. The **petiole** often exhibits the same type of vascular structure as that of the arboreal Papilionaceae, but more complex types also occur. No single type of vascular structure is common to all of the genera and species with pinnate leaves. In transverse sections through the distal end of petioles with wings or well-developed adaxial grooves, the main vascular strand consists of a ventral arc accompanied by a separate dorsal strand between the arms, whilst there are small accessory bundles in the wings. In petioles which are circular or oval in transverse section the vascular system exhibits a considerable diversity of structure (see 'Petiole', p. 491). A sclerenchymatous ring usually surrounds the main petiolar vascular strand and is bounded externally by a sheath of cells containing solitary crystals. Both solitary and clustered **crystals** are present in all parts of the plants. Cluster crystals are particularly characteristic of the mesophyll, thus serving to differentiate the Caesalpinaceae from most Papilionaceae and Mimosaceae, where the crystals are almost invariably solitary. The **pericycle** of the young stem nearly always contains a composite and continuous ring of sclerenchyma, or a continuous ring of fibres. The pericyclic sclerenchyma is frequently accompanied on the outside by a sheath of cells containing solitary crystals. **Grooved stems** occur in certain species of *Cassia*, whilst band-shaped and winged stems are also to be found in various species of *Bauhinia*. **Anomalous secondary thickening** is another characteristic feature of some of the Bauhinias, and includes types with successive growth rings, or, less frequently, with segmented xylem.

(ii) WOOD

Vessels typically mostly solitary, with a few small multiples and irregular clusters; with an oblique or tangential pattern in a few species; ring-porous or semi-ring-porous in a few species and very occasionally with spiral thickening; perforations simple, intervacular pitting alternate and small, pits to parenchyma typically similar but subtending larger pits in a very few species; pits usually vestured; members of medium length to very short. **Parenchyma** usually abundant; typically paratracheal, in round or diamond-shaped sheaths, but in irregular confluent bands or more regular continuous bands in many of the genera; terminal bands present in most of the genera, sometimes broad and conspicuous; broad bands containing intercellular canals present in a few species; a few genera with diffuse strands which often contain 11 or more chambered crystals; strands usually of 2-4 cells, fusiform cells common in some species; storied in several genera. **Rays** 1-7 (mostly 2-3) cells wide or exclusively uniseriate; some genera with narrow procumbent cells, but

relatively fewer than in the Mimosaceae; homogeneous with few uniseriatae in about two-thirds of the genera with multiseriate rays; distinctly storied in several genera. With or without echelon arrangement in the others. **Fibres** with small simple pits; septate in a few genera; of medium length to moderately short. Vertical **intercellular canals** scattered or in bands, normally present in some genera, and traumatic canals present in some others. **Included phloem** of the 'concentric' and 'disperse' types present in a few genera.

LEAF

Generally dorsiventral except in certain species of *Hoffmanseggia* and *Hymenaea*, described as approximately isobilateral in '*Cassia obtusa* Roxb.' by Dastur and Saxton (543). **Hairs** glandular and non-glandular, but the uniseriate type with short basal cells and an elongated distal cell so common amongst the Papilionaceae has been recorded in the Caesalpinaceae only from *Scorodophloeus zenkeri* Harms.

I. Non-glandular

- (a) Unicellular, of various lengths and types. (i) Thin-walled, superficially granulated, shaped like a pruning-hook in *Cassia armata* Wats.; curved in *C. obovata* Collad (Sabnis 1977). (ii) Short, curved like a horn in *Cassia occidentalis* Linn. (iii) Spear-shaped, with tooth-like prongs in *Dialium platysepalum* Bak. (iv) Bracket-shaped or hooked in species of *Apuleia*, *Dialium*, *Labichea*. (v) Two-armed in *Moldenhawera* (two-armed but bicellular in *Bauhinia*).
- (b) Multiseriate, bristle-like in species of *Cassia*.
- (c) Stellate or tufted in species of *Cassia*.
- (d) Branched, resembling a fir-tree in *Cenostigma*.

II. Glandular

- (a) Shaggy, with a glandular, spherical base in certain species of *Cassia* (Fig. 109 A-B). Some of the epidermal cells of the glandular base are themselves elongated to form simple, unicellular hairs in a few species of the same genus.
- (b) Spherical glands, similar to the bases of the hairs described under (a), recorded in species of *Caesalpinia* and *Cassia*.
- (c) Large, club-shaped, visible to the naked eye, occurring on the leaf margin in the *Gleditschieae* and in *Cassia occidentalis*.
- (d) Short-stalked, boat-shaped glands in many species of *Bauhinia* (Fig. 109 c).
- (e) Club-shaped glands with short stalks, smaller than any of the above, recorded in *Apuleia*, *Dialium*, *Sclerolobium*, and *Tachigalia*.
- (f) As (e) but consisting of a glandular base depressed below the leaf surface, and bearing a laterally directed terminal cell in species of *Berlinia*, *Dicorynia*, *Heterostemon*, *Humboldtia* (Fig. 109 d).
- (g) Black glandular dots on the lower surface of the leaf in *Caesalpinia gilliesii* Wall.
- (h) Nectarial glands in *Cassia* sp.
- (i) Pearl glands in *Bauhinia anatomica* Link.

Epidermis papillose or sub-papillose in species of *Apuleia*, *Bauhinia*,

Caesalpinia, *Cassia*, *Crudia*, *Cynometra*, *Delonix* (*Poinciana regia* Boj.), *Detarium*, *Dialium*, *Dicorynia*, *Dimorphandra*, *Hardwickia* (sometimes on both sides), *Labichea*, *Macrolobium*, *Peltophorum*, *Pterolobium*, *Schizolobium*, *Scorodophloeus*, *Wagatea*; mucilaginous in species of *Caesalpinia*, *Cassia*, *Cercidium*, *Cercis*, *Crudia*, *Dialium*, *Dimorphandra*, *Haematoxylon*, *Hoffmanseggia*, *Peltophorum*, *Scorodophloeus*. Epidermal cells containing clustered crystals in *Apuleia* and *Eperua*, and mixed solitary and clustered crystals in *Saraca triandra* Bak. Brown tanniferous masses recorded in the epidermis and

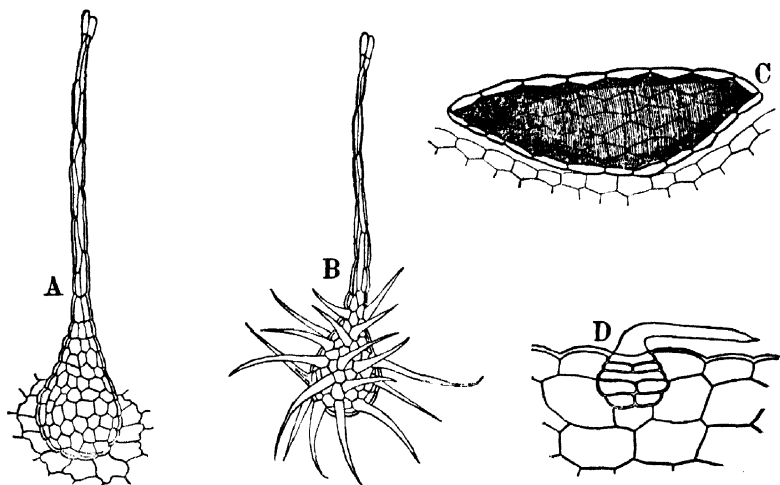


FIG. 109. LEGUMINOSAE—CAESALPINIACEAE

A, Glandular shaggy hair of *Cassia trachycarpa* Vog. B, Glandular shaggy hair of *Cassia aurivilla* Mart. C, Boat-shaped gland with intercellular secretory space of *Bauhinia* sp. D, External gland of the leaf of *Humboldtia* sp.—By Solereder.

hypoderm of *Ceratonia siliqua* Linn. Epidermal cells palisade-like in *Sclerolobium*; divided by thin vertical walls in *Copaifera* (pro parte), *Kingiodendron*, *Oxystigma*, *Prioria*. Epidermis many layered in *Bauhinia confertiflora* Benth. **Hypoderm** recorded on both sides of the leaf in certain species of *Cassia* and in *Dicorynia paraensis* Benth., but not in the closely related *D. floribunda* Spruce; confined to the lower side in species of *Ceratonia*, *Cercidium*, and *Parkinsonia*.

Stomata usually confined to the lower surface, but recorded on the upper side in species of *Caesalpinia*, *Cassia*, *Cercidium*, *Erythrophleum* (only in one species). Arrangement of the subsidiary cells very variable even within a species, distinct types having been observed side by side in a single leaf in certain instances. Rubiaceous stomata commonly but not invariably present in *Afzelia*, *Amherstia*, *Apuleia*, *Berlinia*, *Brownea*, *Caesalpinia* (pro parte), *Campsiandra*, *Cassia*, *Cenostigma*, *Copaifera*, *Crudia*, *Cynometra*, *Dialium*, *Dicorynia*, *Delonix* (*Poinciana regia*), *Dimorphandra* (pro parte), *Diptychandra*, *Eperua*, *Erythrophleum* (one subsidiary cell smaller than the other), *Haematoxylon*, *Hardwickia*, *Heterostemon*, *Hoffmanseggia*, *Humboldtia*, *Hymenaea*, *Macrolobium*, *Mezoneurum*, *Moldenhawera*, *Peltogyne*, *Peltophorum*, *Prioria*, *Pterolobium*, *Saraca*, *Schizolobium*, *Schotia* (pro parte), *Sclerolobium*, *Scorodo-*

phloeus, *Tachigalia*, *Tamarindus*, *Trachylobium*, *Wagatea*. Subsidiary cells generally absent from *Caesalpinia* (pro parte), *Ceratonia*, *Cercidium*, *Cercis*, *Dimorphandra*, *Gleditschia*, *Gymnocladus*, *Labichea*, *Parkinsonia*, *Peltophorum*, *Poeppigia*, *Schotia* (pro parte).

Mesophyll. Sometimes containing stone cells in *Macrolobium* and *Saraca*. Sclerenchymatous fibres recorded in species of *Cynometra*, *Heterostemon*, *Saraca*, and *Schotia*, often appearing as transparent dots (either in the whole leaf or after cutting transversely), the bulbous bases of the fibres abutting on the vascular bundles and filled with silica. Fibres unite the upper and lower epidermis like girders in some species. Sclereids of an unspecified nature recorded by Russell and Hédin (1974) and Russell (1971) in *Pterygopodium oxyphyllum* Harms. Transparent dots also caused by the presence of groups of silicified cells in *Apuleia praecox* Mart.

Vascular bundles of the **veins** usually accompanied by sclerenchyma; embedded in the mesophyll or vertically transcurrent. Embedded in *Afzelia*, *Berlinia*, *Caesalpinia*, *Cassia*, *Cercidium*, *Cercis* (pro parte), *Crudia*, *Cynometra*, *Delonix* (*Poinciana regia*), *Dialium* (pro parte), *Dimorphandra* (pro parte), *Gleditschia*, *Gymnocladus*, *Haematoxylon*, *Heterostemon*, *Hoffmanseggia*, *Macrolobium*, *Mezoneurum*, *Moldenhawera*, *Parkinsonia*, *Peltogyne*, *Peltophorum*, *Poeppigia*, *Prioria*, *Pterogyne*, *Pterolobium*, *Saraca*, *Schizolobium*, *Schotia*, *Tamarindus*; vertically transcurrent in *Apuleia*, *Brownea*, *Campsiandra*, *Cenostigma*, *Cercis* (pro parte), *Copaifera*, *Didium* (pro parte), *Dicorynia*, *Dimorphandra* (pro parte), *Diptychandra*, *Eperua*, *Hardwickia*, *Humboldtia*, *Hymenaea*, *Labichea*, *Peltophorum*, *Sclerolobium*, *Tachigalia*, *Trachylobium*, *Wagatea*.

Petiole. Examination of the limited number of slides in the collection at Kew has revealed the following information concerning the structure to be seen in transverse sections through the distal end. For a very detailed account of the petiole structure in a number of Caesalpinaceae see Morvillez (1958) and Watari (2364). Main vascular strand cylindrical, but sometimes having distinct dorsal and ventral portions, the latter usually being in the form of an open arc and the dorsal part variously shaped according to the species. The line of demarcation between these two types is not always clearly defined. Xylem in both types of vascular strand more continuous in some species than in others. Main vascular strand usually separated or tending to be separated into dorsal and ventral portions as just described in *Bauhinia fornicata* Link. (Fig. 118 J), *Cassia grandis* Linn., *Cercis siliquastrum* Linn., *Gleditschia capsica* Desf., *G. japonica* Miq., *Schotia latifolia* Jacq., *Tamarindus indica* Linn.; more perfectly cylindrical in *Caesalpinia japonica* Sieb. et Zucc., *Gymnocladus dioica* K. Koch., *Haematoxylon campechianum* Linn., *Saraca declinata* Miq. (Fig. 118 F). Vascular structure distinctive in *Brownea coccinea* Jacq. (Fig. 118 G). Additional accessory strands present in the wings in the above species of *Bauhinia*, *Cassia*, *Gleditschia*, *Tamarindus*, in the 'cortex' in *Brownea* and *Cercis* and enclosed within the main vascular strand in *Saraca*. Vascular tissue strongly supported by pericyclic fibres, accompanied externally by cells containing solitary crystals, in all of the species examined. Stone cells present in the cortex and pericycle of *Brownea*.

Secretory elements of various types widespread, but according to Solereder the tannin sacs, so characteristic of the Papilionaceae, are rare.

There seems to be considerable confusion concerning the chemical nature of the contents of the secretory cells in the family, and the subject needs further investigation.

- I. Secretory cells, ellipsoidal when situated in the palisade tissue and causing pellucid dots in the leaf; spherical when situated in the spongy mesophyll.
 - (a) With brown tanniniferous contents in *Cassia* and *Erythrophleum* (around the vascular system).
 - (b) With pale-yellow contents in *Caesalpinia* (certain species mostly included in the sections *Coulteria*, *Guilandina*, and *Nugania*), *Diptychandra*, *Mezoneurum*, *Pterolobium*, *Wagatea*.
 - (c) Containing mucilage in certain species of *Berlinia*, *Cassia*, *Cercidium*, *Macrolobium*, *Peltogyne*.
 - (d) Secretory cells with unidentified but apparently tanniniferous contents present in the phloem and usually in the 'cortical' and 'medullary' regions of the petiole in most of the rather limited material in the Kew slide collection.
- II. Secretory cavities, usually lined with a distinct epithelium.
 - (a) Containing yellow resin and causing transparent dots in the leaves in *Copaifera*, *Eperua*, *Hymenaea*, *Peltogyne*, *Prioria*, *Trachylobium*.
 - (b) With brown tanniniferous contents, causing opaque dots on the leaf in species of *Caesalpinia* and *Cenostigma*.
 - (c) With unspecified contents in *Daniella*, *Detarium*, *Hardwickia*, *Kingiodendron*, *Oxystigma*, and, according to Russell and Hédin (1974), in the parenchymatous tissues of the lamina and petiole in *Gossweilerodendron* and *Pterygopodium*.

Crystals (see also under 'Epidermis' and 'Petiole'). Clusters common, especially in the mesophyll, thus serving to differentiate the Caesalpinieae from most Papilionaceae and Mimosaceae. Solitary crystals chiefly associated with the veins; sometimes occurring as well in local swellings of the cell wall of the palisade tissue in species of *Eperua*, *Macrolobium*, *Tachigalia*, *Tamarindus*.

AXIS

YOUNG STEM

Cork not very fully investigated; arising superficially in species of *Bauhinia*, *Brownea*, *Caesalpinia*, *Cassia*, *Ceratonia*, *Cercis*, *Gleditschia*, *Gymnocladus*, *Haematoxylon*, *Saraca*, *Schotia*, *Tamarindus*, and in the second or third layer of the primary cortex in *Gleditschia*. Cork cells greatly flattened in *Gleditschia* and *Tamarindus*, less so in *Bauhinia* and *Gymnocladus*, cubical in *Cassia* and *Ceratonia*; thin-walled in *Bauhinia* and *Gleditschia*, but thicker in *Gymnocladus*; thickened on the outer tangential wall in *Tamarindus* and on the inner tangential wall in *Ceratonia*. Sclereids recorded by Planchon (1729) in the cork of *Erythrophleum*. Outer part of the primary **cortex** occasionally collenchymatous; stone cells recorded in this region in species of *Brownea*, *Erythrophleum*, *Gleditschia*, *Gymnocladus*. **Endodermis** present as a well-defined starch sheath in *Cercis siliquastrum* Linn. **Pericycle** almost invariably containing a composite and continuous ring of sclerenchyma, except rarely in

Bauhinia. A continuous zone of fibres which becomes interrupted when older has also been recorded in *Erythrophleum*. Secondary **phloem** frequently containing fibres, e.g. in *Brownea coccinea* Jacq. and *Tamarindus indica* Linn.; occasionally stratified into hard and soft portions, e.g. in *Cassia grandis* Linn.; often containing solitary crystals, occasionally accompanied by clusters. Portions of the rays passing through the phloem frequently broadened towards the exterior. **Xylem** in the form of a continuous cylinder traversed by narrow rays; interrupted by broader rays in some species. Vessels with simple perforations. **Secretory elements**. An oil, containing sulphur and smelling of garlic, is present in the form of a glucoside in the primary cortex of *Scorodophloeus zenkeri* Harms. The glucoside accompanied by an enzyme occurs in cells which are deeply stained when treated with iodine. Short oil cavities also stated to occur in the primary cortex of *Copaifera* spp., and elongated secretory cavities in the same position in species of *Caesalpinia*, *Daniella*, *Detarium*, *Hardwickia*, *Kingiodendron*, *Oxystigma*, *Schotia*. Similar cavities recorded in the pith and/or pericycle as well in *Detarium*, *Erythrophloeum densiflorum* (Elm.) Merr., but according to Planchon (1729) not in other species of *Erythrophleum*, and *Hardwickia*. Fusiform secretory cavities recorded in the cortex, xylem, and pith of certain species of *Gossweilerodendron* and in *Pterygopodium* by Russell and Hédin (1974). Secretory canals occur in the primary cortex of *Eperua falcata* Aubl., and in the pith of species of *Copaifera*, *Daniella*, *Oxystigma*, *Prioria*. Secretory cells, filled with material believed to be tanniferous, observed in the cortex, phloem, rays, and pith of *Brownea coccinea*, *Cercis siliquastrum*, *Saraca declinata* Miq., *Tamarindus indica* and in the phloem only in *Cassia grandis* and *Haematoxylon campechianum* Linn. Cells with mucilaginous walls and contents which are stained pink by safranin, also seen in the cortex and pith of *Schotia latifolia* Jacq. and in the pith of *Saraca declinata*. Both solitary and cluster **crystals** common, solitary types being especially frequent in the cortex in material represented in the slide collection at Kew. See also under 'Phloem'.

WOOD (Fig. 110)

Vessels typically medium-sized (100–200 μ mean tangential diameter); very small (25–50 μ) in *Libidibia*, *Poeppigia*, and *Zuccagnia*; moderately small (50–100 μ) in *Apuleia*, *Baikiaea*, *Caesalpinia*, *Cercidium*, *Copaifera mopane* Kirk., *Cynometra alexandri* C. H. Wright, *Etaballia*, *Holocalyx*, *Parkinsonia*, *Peltogyne*, and *Pseudocopaiva*; large (more than 200 μ) in some species of *Abauria*, *Acrocarpus*, *Afzelia*, *Aldina*, *Berlinia*, *Cassia*, *Cordyla*, *Daniella*, *Detarium*, *Dialium*, *Dinizia*, *Eperua*, *Erythrophleum*, *Koompassia*, *Mora*, *Peltophorum*, and *Sclerolobium*, typically solitary with a few multiples of 2 or 3 cells and some irregular clusters; these clusters, usually of small cells, not always present in every section, but a tendency to produce them locally appears to be characteristic of most of the genera; radial multiples more common and sometimes of 4 or more cells in *Apuleia*, *Baikiaea*, *Bauhinia* p.p., *Burkea*, *Caesalpinia*, *Cercidium*, *Cercis*, *Copaifera* p.p., *Cynometra*, *Holocalyx*, *Libidibia*, *Parkinsonia*, and *Zuccagnia*; with an oblique pattern, distinct in *Zuccagnia* (Fig. 110 B), and rather vague in *Gleditschia*; clusters more pronounced and forming broken lines in the late wood of *Cercis* and *Gymnocladus* (Fig. 110 C); mostly between 1.5 and 5 per mm.; 5–20 per mm. in some species of *Brownea*,

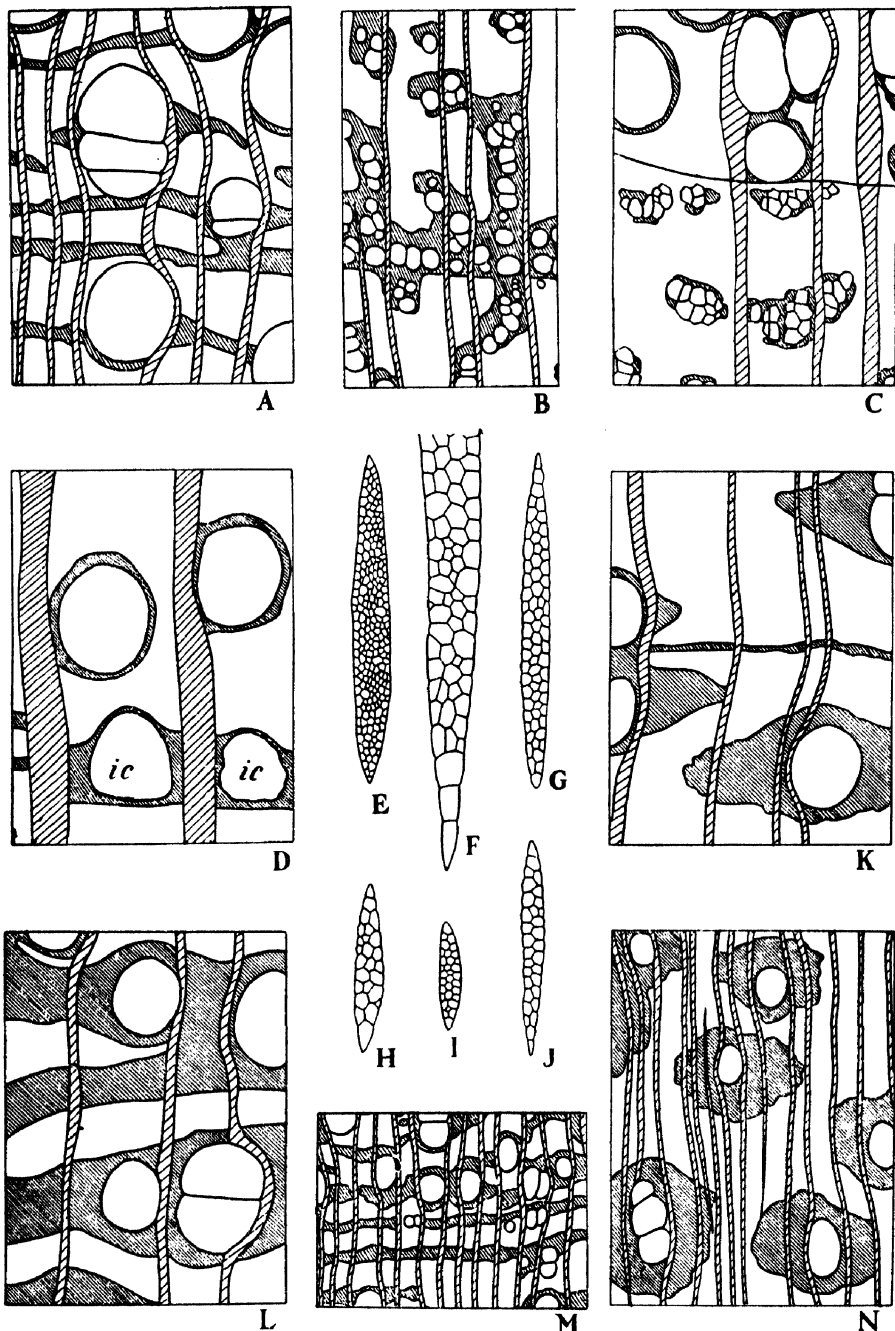


FIG. 110. LEGUMINOSAE—CAESALPINIACEAE

A, *Dialium kingii* Prain. B, *Zuccagnia punctata* Cav. C, *Gymnocladus canadensis* Lam. D, *Eperua falcata* Aubl. E, *Gleditschia japonica* Miq. F, *Eperua falcata* Aubl. G, *Gossweilerodendron balsamifera* Harms. H, *Baikiaea pluriyuga* Harms. I, *Holocalyx balansae* Micheli. J, *Azelia bakeri* Prain. K, *A. bakeri* Prain. L, *Cassia siamea* Lam. M, *Cynometra alexandri* C. H. Wright. N, *Tamarindus indica* Linn.

i.c. Intercellular canals

Burkea, *Caesalpinia*, *Chidlowia*, *Copaifera*, *Cryptosepalum*, *Cynometra*, *Dicymbe*, *Haematoxylon*, *Hardwickia*, *Hymenostegia*, *Melanoxylon*, *Parkinsonia*, *Peltogyne*, and *Pseudocopaiva*, 21–40 per mm. in some species of *Apuleia*, *Brasilettia*, *Browneopsis*, *Caesalpinia*, *Campsiandra*, *Mezoneuron*, *Peirania*, *Poeppigia*, and *Pseudocopaiva*, more than 40 per mm. in *Baikiaea plurijuga* Harms. and some specimens of *Cynometra alexandri*; ring-porous or semi-ring-porous in species of *Asacara* (1886), *Caesalpinia*, *Cercidium*, *Cercis*, *Gleditschia*, *Gymnocladus*, *Parkinsonia* (1851), *Trachylobium*, and *Zuccagnia* (1886); spiral thickening present in *Cercis*, *Gleditschia*, *Gymnocladus*, and *Zuccagnia* (1864). Perforations simple. Intervascular pitting alternate, small; very small in *Bauhinia* p.p., *Caesalpinia*, *Copaifera* p.p., *Crudia*, *Cynometra*, *Dimorphandra*, *Hardwickia*, *Holocalyx*, *Humboldtia*, *Intsia*, *Peltogyne*, *Saraca*, and *Zuccagnia*, minute in *Browneopsis*, *Chidlowia*, *Delonix*, *Elizabetha*, *Hymenostegia*, *Macrolobium*, and *Mora*; moderately large in *Aldina* and *Martiodendron*; occasionally with marked striations due to coalescent apertures, e.g. in *Acrocarpus*, *Holocalyx*, *Parkinsonia*, and *Zuccagnia*; pits to parenchyma and ray cells similar to the intervascular pits, but subtending occasional larger oblong pits in the parenchyma walls in *Bauhinia*, *Burkea*, *Cercidium*, and *Copaifera* p.p. Record and Hess (1886) note unilaterally compound pitting in *Batesia*, *Cynometra*, *Eperua*, *Jacqueshuberia*, and *Parkinsonia*. Pits vested except in the Bauhinieae, i.e. *Bauhinia* and *Cercis*. Solid deposits present in nearly all the species, tyloses rare, observed or reported in *Bauhinia malabarica* Roxb., *Gleditschia formosana* Hay. (1209) and *Melanoxylon brauna* Schott. (1894). Mean member length 0.2–0.5 mm. **Parenchyma** usually moderately abundant and predominantly paratracheal; most typically as a sheath, several cells wide, about the vessels, round, diamond shaped or distinctly aliform in cross-section and often locally confluent where the vessels are close together (Fig. 110 K, and N); with considerable variation within these limits in different parts of the ring and in different specimens; commonly rounded (vasicentric) in *Batesia*, *Brachystegia* p.p., *Brasilettia*, *Ceratonia*, *Cercidium*, *Cercis*, *Chamaesenna*, *Conzattia*, *Copaifera* p.p., *Dicymbe*, *Dimorphandra*, *Englerodendron*, *Eperua*, *Gymnocladus*, *Heterostemon*, *Intsia* p.p., *Parkinsonia*, *Peltophorum* p.p., *Prioria*, *Pseudocassia*, *Pterogyne* p.p., *Schizolobium*, *Schotia*, *Sindora*, *Tachigalia*, *Vouapa*, and *Zuccagnia*; predominantly aliform and most typically diamond shaped in *Acrocarpus*, *Afzelia*, *Berlinia*, *Brachystegia* (most species), *Brownea*, *Bussea*, *Caesalpinia*, *Campsiandra*, *Cassia* p.p., *Copaifera* p.p., *Cordyla*, *Daniella*, *Detarium*, *Dinizia*, *Erythrophleum*, *Goniorrhachis*, *Gossweilerodendron*, *Hardwickia*, *Hymenaea*, *Intsia* p.p., *Isobertinia*, *Koompassia* p.p., *Macrolobium*, *Melanoxylon*, *Mezoneuron*, *Mildbraediodendron*, *Mora*, *Oxystigma*, *Pahudia*, *Peirania*, *Pterogyne* p.p., *Recordoxylon*, *Saraca*, *Sclerolobium*, *Tamarindus*, and *Trachylobium*; in irregular confluent bands in *Afzelia quanzensis* Welw., *Aldina*, *Amphimas*, *Baikiaea*, *Bauhinia*, *Campsiandra*, *Cassia* p.p. (Fig. 110 L), *Chidlowia*, *Cynometra*, *Dicorynia*, *Distemonanthus*, *Gleditschia*, *Haematoxylon*, *Holocalyx*, *Koompassia*, *Peltogyne*, and *Peltophorum* p.p.; intermediate between the above and aliform in *Burkea*, *Cassia* p.p., *Cryptosepalum*, *Elizabetha*, *Humboldtia*, *Kingiodendron*, *Mora*, and *Pseudocopaiva*; in more regular bands that are difficult to classify in *Abauria*, *Apuleia*, *Cassia* p.p., *Crudia*, *Cynometra* p.p. (Fig. 110 M), *Dialium*, *Etaballia* (accompanied by abaxially aliform),

Hymenostegia, *Pterygopodium* (containing ducts), *Sciaccasia*, *Stahlia*, *Storckia*, and *Zollernia*; scanty paratracheal in *Jacqueshuberia* (1836); scattered strands (diffuse), without crystals, present in *Aldina*, *Campsiandra* (sometimes absent) *Ceratonia*, *Dinizia*, *Gossweilerodendron*, *Holocalyx*, *Pterogyne*, and *Recordoxylon*, and containing chambered crystals in *Bauhinia* p.p., *Bussea*, *Cercidium*, *Copaifera* p.p., *Crypterosepalum*, *Englerodendron*, *Hardwickia*, *Humboldtia*, *Peltophorum*, *Saraca*, *Schotia*, *Sindora*, and *Tamarindus*; regular broad bands containing vertical intercellular canals present in addition to the above in some species (see below); terminal parenchyma present in most species. Chambered crystals present in (a) scattered strands, in the genera listed above, and (b) in the margins of the paratracheal or banded parenchyma of many of the genera; chambered crystals not observed in *Batesia*, *Brasilettia*, *Brownea*, *Browneopsis*, *Campsiandra*, *Ceratonia*, *Chamaesenna*, *Chidlowia*, *Dicorynia*, *Didelotia*, *Dinizia*, *Elizabetha*, *Erythrophleum*, *Gleditschia*, *Gymnocladus*, *Martiodendron*, *Peltophorum* p.p., *Poeppigia*, *Pterogyne*, and *Schizolobium*; the maximum number of crystals per strand seldom fewer than 11 and often many more; with 2-4 large crystals per strand in *Etaballia*; chambered strands sometimes locally biseriate (radial section) in *Prioria copaifera* Gris.; with sclerotic cells in *Martiodendron excelsa* (Benth.) Gleason; cells sometimes containing gum-like deposits. Record and Hess (1886) note 'inflated cells' in *Batesia*, and gum cysts in *Poincianella*. Strands most commonly of 2-4 cells, up to 8 cells in some species of *Cynometra*, *Dicorynia*, and *Koompassia*; fusiform parenchyma cells moderately common in some species of *Copaifera*, *Dinizia* (diffuse cells only), *Kingiodendron*, *Macrolobium*, and *Pterogyne*, not observed in woods with heterogeneous rays. Storied in many of the genera, e.g. in some species of *Afzelia*, *Aldina*, *Apuleia*, *Baikiaea*, *Brachystegia*, *Caesalpinia*, *Cercis*, *Copaifera*, *Cordyla*, *Cynometra*, *Daniella*, *Dialium*, *Dicorynia*, *Distemonanthus*, *Etaballia*, *Haematoxylon*, *Holocalyx*, *Hymenaea*, *Kingiodendron*, *Mildbraediodendron*, *Oxystigma*, *Peltogyne*, *Prioria*, *Pterogyne*, *Pterygopodium*, *Tamarindus*, *Zollernia*, and *Zuccagnia*. In *Poeppigia procera* Presl., scattered among the septate fibres in groups and bands, there are thin-walled, septate parenchyma strands; these strands are distinctly shorter than the surrounding septate fibres, the lumina wider and the pits rounded instead of slit-like. With marked intercellular spaces in *Aldina insignis*. **Rays** mostly 2-3 cells wide, exclusively uniseriate or with only a few biseriate rays in some species of *Bauhinia*, *Brachystegia*, *Brownea*, *Browneopsis*, *Cassia*, *Chidlowia*, *Crudia*, *Cynometra*, *Dicymbe*, *Dimorphandra*, *Elizabetha*, *Englerodendron*, *Erythrophleum fordii* Oliv. (1206), *Etaballia*, *Heterostemon*, *Humboldtia*, *Ibadja* (1615), *Isobertinia*, *Jacqueshuberia* (1836), *Loesenera*, *Macrolobium*, *Oxystigma*, *Poincianella*, and *Tachigalia*; 4-7 cells wide in some species of *Acrocarpus*, *Amphimas*, *Burkea*, *Ceratonia*, *Cercidium*, *Cercis* (2158), *Copaifera*, *Cynometra* (1154), *Daniella*, *Detarium*, *Dicorynia*, *Distemonanthus*, *Eperua*, *Gleditschia*, *Gossweilerodendron*, *Gymnocladus*, *Haematoxylon*, *Hardwickia*, *Hymenaea*, *Melanoxylon*, *Parkinsonia*, *Peltogyne*, *Schotia*, *Schizolobium*, and *Trachylobium*; of 2 distinct sizes in *Eperua*; less than 1 mm. high, except in *Eperua* and *Prioria*; woods with multiseriate rays often with few uniseriates, but genera with moderately numerous uniseriates more common than in the *Mimosaceae*, e.g. *Bauhinia*, *Berlinia*, *Campsiandra*, *Cassia*, *Cercis*, *Cynometra*, *Daniella*, *Detarium*, *Elizabetha*, *Eperua*, *Gossweilerodendron*, *Haematoxylon*,

Hymenostegia, *Krugiodendron*, *Mora*, *Parkinsonia*, *Peltophorum*, *Poeppigia*, *Prioria*, *Saraca*, *Schotia*, *Tamarindus*, *Trachylobium*, *Vouapa*, and *Zuccagnia*; mostly from 4 to 12 rays per mm.; 13 to 20 per mm. in some species of *Apuleia*, *Bauhinia*, *Brachystegia*, *Browneopsis*, *Cercis*, *Cynometra*, *Elizabetha*, *Heterostemon*, *Holocalyx*, *Hymenostegia*, *Ibadja* (1615), *Libidibia*, *Poeppigia*, *Stahlia*, *Storckiiella*, and *Tamarindus*, fewer than 4 per mm. in *Eperua*, *Gleditschia*, *Gymnocladus*, and *Hymenaea*; homogeneous (Kribs's Types I, II, and III) in *Afzelia*, *Aldina*, *Amphimas*, *Baikiaea*, *Batesia*, *Berlinia* p.p., *Brachystegia*, *Brasilettia*, *Burkea*, *Bussea*, *Caesalpinia*, *Campsiandra*, *Cassia*, *Cercidium*, *Chamaesenna*, *Chidlowia*, *Conzattia*, *Copaifera*, *Cordyla*, *Cynometra* (except *C. ramiflora* (1154)), *Dialium*, *Dicymbe* p.p., *Didelotia*, *Dimorphandra*, *Dinizia*, *Erythrophleum*, *Gleditschia*, *Goniorrhachis*, *Gossweilerodendron*, *Gymnocladus*, *Haematoxylon*, *Hardwickia*, *Hymenaea*, *Intsia*, *Libidibia*, *Martiodendron*, *Melanoxylon*, *Mezoneuron*, *Oxystigma* p.p., *Pahudia*, *Parkinsonia*, *Peiranisia*, *Peltogyne*, *Peltophorum*, *Poeppigia*, *Poincianella*, *Pseudocassia*, *Pterogyne*, *Schizolobium*, *Sciacassia*, *Sclerolobium*, *Stahlia*, *Storckiiella*, *Tachigalia*, *Tamarindus*, and *Zuccagnia*; heterogeneous (Kribs's Types II and III), with 1-2 marginal rows of upright cells in the other genera and with up to 4 rows in *Eperua*; procumbent cells small in tangential diameter (less than 10 μ) in some genera, e.g. *Brachystegia*, *Bussea*, *Caesalpinia*, *Cassia*, *Cercidium*, *Cercis*, *Cynometra*, *Dialium*, *Dinizia*, *Distemonanthus*, *Erythrophleum*, *Gleditschia* (Fig. 110 E), *Goniorrhachis*, *Gossweilerodendron*, *Gymnocladus* p.p., *Haematoxylon*, *Holocalyx*, *Hymenaea*, *Koompassia*, *Mora* p.p., *Parkinsonia*, *Peltogyne*, *Poeppigia*, *Pterogyne*, *Schizolobium*, *Tamarindus*, and *Zuccagnia*; containing gum-like deposits in most species; crystals rare, observed only in *Abauria*, *Acrocarpus*, *Caesalpinia* p.p., *Cordyla*, *Cynometra* p.p., *Humboldtia*, *Krugiodendron*, *Pterogyne*, and *Zuccagnia*. Many genera without any distinct tendency to arrangement in echelon or stories, but distinctly storied in some species of *Afzelia*, *Aldina*, *Amphimas*, *Apuleia*, *Baikiaea*, *Bauhinia*, *Brachystegia*, *Brasilettia*, *Caesalpinia*, *Cercis*, *Cordyla*, *Crudia*, *Cynometra*, *Daniella*, *Delonix*, *Dialium*, *Dicorynia*, *Distemonanthus*, *Erythrophleum*, *Etaballia*, *Goniorrhachis*, *Haematoxylon* (1851), *Holocalyx*, *Koompassia*, *Lecointea*, *Libidibia*, *Martiodendron*, *Melanoxylon*, *Mildbraediodendron*, *Pahudia*, (1851), *Peltogyne*, *Poeppigia*, *Poincianella*, *Pseudocopaiva*, *Pterogyne*, *Stahlia*, *Storckiiella*, *Tamarindus*, and *Zollernia*. In several genera in which the other elements are storied, the rays are commonly 2 or 3 stories high, and in consequence are not themselves distinctly storied. **Fibres** with few small, simple pits, more numerous on the radial than on the tangential walls. Septate in *Batesia*, *Brasilettia*, *Bussaea*, *Cassia*, *Ceratonia*, *Distemonanthus*, *Peltophorum*, *Poeppigia*, *Poinciana* (1886), and *Schizolobium*. Walls usually moderately to very thick, but thin in some species of *Acrocarpus*, *Afzelia*, *Cercidium*, *Intsia*, *Prioria*, *Saraca*, and *Schizolobium*; commonly with a gelatinous inner layer and often with dark gum-like contents. Bands of thin-walled fibres resembling parenchyma on cross-section present in *Poeppigia* (1886). Mean length 0.7-1.4 mm. **Intercellular canals** occur regularly in bands in some species of *Copaifera*, *Detarium*, *Eperua* (Fig. 110 D), and *Sindora* and scattered in *Daniella*, *Gossweilerodendron*, *Kingiodendron*, *Prioria*, and *Pterygopodium*; Record (1851) notes canals of 'normal vertical type' in *Oxystigma*, though absent from *O. stapfiana* A. Chev. (461); vertical traumatic canals have been recorded (1851) in *Berlinia*,

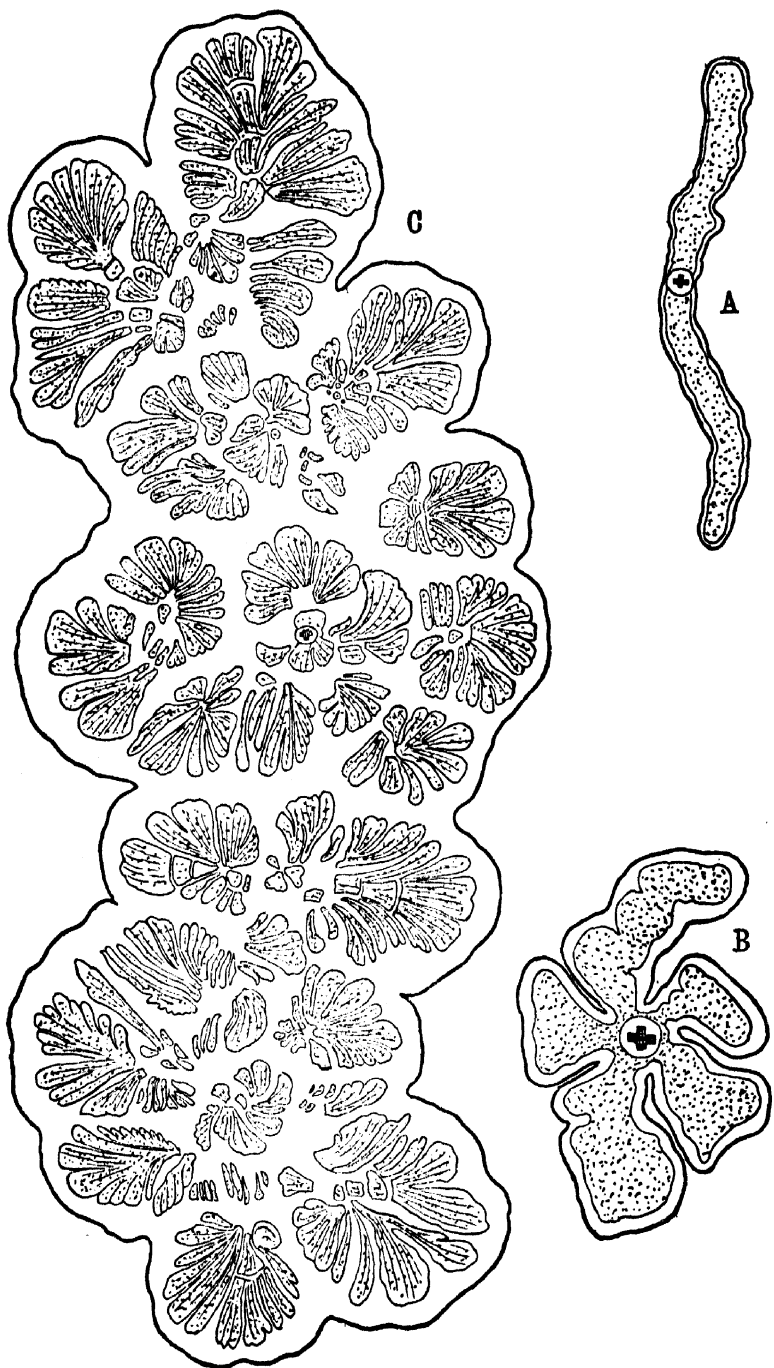


FIG. 111. LEGUMINOSAE—CAESALPINIACEAE

A, Winged and undulated stem of *Bauhinia* sp. (H. Schenck, collection of woods, no. 167). B, *Bauhinia rubiginosa* Bong. C, Split xylem-mass of *Bauhinia langsdorffiana* Bong. A and B, natural size. C, approximately natural size.—After H. Schenck.

Cercidiopsis, *Hardwickia*, *Hymenaea*, *Macrolobium*, and *Peltogyne*. **Included (interxylary) phloem** occurs in certain genera. See 'Anomalous Structure' below. **Growth rings** and the seasonal development of the wood have been investigated by Coster (481) in *Bauhinia*, *Cassia*, *Peltophorum*, *Poinciana*, and *Tamarindus*. Besson (186) records a very high silica content in *Dicorynia* and *Dialium* and a high ash content in the latter.

ROOT

For information concerning **bacteria** in the roots of *Gleditschia triacanthos* Linn. see Friesner's (720) account. Fusiform **secretory cavities** recorded by Russell and Hédin (1974) in the cortex and xylem of *Gossweilerodendron* and *Pterygopodium*. Well-developed cork, a broad region of phloem and pericycle, strands of fibres, and conspicuous rays in the phloem recorded by Dastur and Saxton (543) in the older parts of the long tap-roots of *Cassia auriculata* Linn.

ANOMALOUS STRUCTURE

Apart from species of *Cassia* with grooved stems, anomalous structure is confined to certain species of *Bauhinia*. The following types are recorded by Solereder.

- A. Band shaped and winged stems (Fig. 111 A-B) in '*Bauhinia blumenaviana* H. Schenck. and other species of *Bauhinia*'. Stems becoming band shaped during thickening, owing to the cambium being confined to 2 opposed arcs. Wings and ribs arising subsequently on the broad sides of older stems. Perimedullary part of the wood forming a cruciate ring, denser in structure than the remainder.
- B. Successive rings of growth recorded in *B. angulosa* Vig., *B. rubiginosa* Bong., and *B. vahlii* W. et A.
- C. Xylem becoming fissured, firstly owing to dilation of the thin-walled xylem parenchyma, each segment of wood subsequently becoming surrounded by a cambium which produces xylem internally and phloem externally. Secondary fissures also occur. The central xylem mass sometimes becomes broken. This type recorded with certainty only in *Bauhinia langsdorffiana* Bong. (Fig. 111 C).

Handa (885, 886) has described several types of anomalous thickening in *Bauhinia*. In *B. japonica* Maxim. the three following types occur. (1) Dilation tissue, originating in the pith and xylem, splits up the central area of the stem. Vascular bundles provided with cambium then arise in the dilation tissue. This anomaly occurs towards the base of the stem. (2) The axial and periaxial portions of the xylem become separated by dilation parenchyma in which small vascular bundles, often arranged in 2 rows, subsequently arise. The bundles of the inner row are normally, and of the outer row inversely, orientated. This occurs immediately above the stem base. (3) Numerous vascular bundles are differentiated in dilation parenchyma situated in the pith and inner part of the xylem of the roots, especially those which are tuberous. Thick axes of *B. championi* Benth. exhibit a cleft xylem mass and 1 or 2 successive rings of xylem and phloem. Secondary bundles arise in the dilation tissue in the pith. Each segment of xylem becomes surrounded by an almost continuous ring of cambium, the activity of which combined with that of the

secondary bundles causes the xylem mass to become considerably dissected. Later on successive rings of xylem and phloem are produced from meristems which probably originate in the pericycle. For other work on the stem structure of *Bauhinia* see Löffler (1388) and Wagner (2343). Included phloem of the 'concentric' type (*c.l. circumvallatum*) observed in some species of *Koompassia*, e.g. *K. excelsa* Ridl. and *K. malaccensis* Benth. and reported by Record (1881) in one rather doubtful species of *Dicyme*.

TAXONOMIC AND PHYLOGENETIC NOTES

see under Papilionaceae, p. 527.

ECONOMIC USES

Edible fruits derived from members of the Caesalpinaceae include the Carob or Locust Bean (*Ceratonia siliqua* Linn.), Tamarinds (*Tamarindus indica* Linn.), the Kentucky Coffee Tree (*Gymnocladus canadensis* Lam.). Tannin occurs in many species and has been extracted for use from *Caesalpinia* and *Cassia*. Copaiba balsam is derived from species of *Copaifera*. Senna pods and leaves, used in medicine, are obtained from species of *Cassia*. The most important kind is Alexandrian Senna (*C. acutifolia* Del.) which is considered to be superior to Arabian or Tinnevely Senna (*C. angustifolia* Vahl.). The leaves of other species of *Cassia* are sometimes used as substitutes. The bark of *Erythrophleum guineense* G. Don, used as an arrow poison in West Africa, has also been employed as an anaesthetic in dentistry.

Senna leaves can be recognized by the following characters: the thick-walled unicellular trichomes; the cells of the epidermis which are sometimes horizontally divided and mucilaginous; the mostly rubiaceous stomata on both surfaces; the isobilateral mesophyll with a single layer of palisade cells towards each surface; the spongy tissue in the centre of the mesophyll containing cluster crystals of calcium oxalate; the vascular bundles accompanied by fibres above and below, with cells containing solitary crystals situated externally to the fibre groups. Various attempts have been made to devise methods of distinguishing the powdered leaves of *C. acutifolia* from those of *C. angustifolia*. Levin (1360) found that the average vein-islet number is 26 for *C. acutifolia* and 21 for *C. angustifolia*. Saber (1976) found that the epidermal area per gramme was not sufficiently constant to serve as a basis for separating the 2 species, but George (755) was more successful when using variations in palisade ratios. Gilg and Schuster (780) state that the leaflets of *Cassia auriculata* Linn. have been substituted for those of genuine senna. The substitute leaflets have a dorsiventral mesophyll with 2 layers of palisade cells. Voigt (2339) records that powdered senna has been found with an admixture of *Belladonna*.

The most characteristic anatomical features of the bark of *Erythrophleum guineense* include the very numerous large groups of sclerenchymatous cells; the stone cells and fibres in the pericycle; the tanniferous cells.

The woods of this family are often very durable and many are distinctively coloured; some indeed have been important sources of dyes, e.g. Logwood, *Haematoxylon campechianum* L., and Brazilwood, *H. brasiletto* Karst.

Several of the timbers are widely known, e.g. West Indian Locust, *Hymenaea courbaril* L., Purpleheart, *Peltogyne* spp., Bubinga, *Copaifera* spp., and

'Rhodesian teak', *Baikiaea plurijuga* Harms. The timbers of many other species or genera are of local importance.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Afzelia, Amherstia, Apuleia, Bauhinia,* Berlinia, Brownea,* Caesalpinia,* Campsiandra, Cassia,* Caulotretus, Cenostigma, Ceratonia, Cercidium, Cercis,* Copaifera, Crudia, Cynometra, Daniella, Delonix, Detarium, Dialium, Dicorynia, Dimorphandra, Diptychandra, Eperua, Erythrophleum, Gleditschia,* Gossweilerodendron, Gymnocladus,* Haematoxylon,* Hardwickia, Heterostemon, Hoffmanseggia, Humboldtia, Hymenaea, Kingiodendron, Labichea, Macrobium, Mezoneuron, Moldenhawera, Oxystigma, Parkinsonia, Peltogyne, Peltophorum, Poeppigia, Poinciana, Pomarea, Prioria, Pterogyne, Pterolobium, Pterygopodium, Saraca,* Schizolobium, Schotia,* Sclerolobium, Scorodophloeus, Tachigalia, Tamarindus,* Trachylobium.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Abauria, Acrocarpus, Afzelia, Amphimas, Apuleia, Baikiaea, Batesia, Bauhinia, Berlinia, Brachystegia, Brasilettia, Brownea, Browneopsis, Burkea, Bussea, Caesalpinia, Campsiandra, Cassia, Ceratonia, Cercidium, Cercis, Chamaesenna, Chidlowia, Conzattia, Copaifera, Cordyla, Crudia, Cynometra, Daniella, Delonix, Detarium, Dialium, Dicorynia, Dicymbe, Didelotia, Dimorphandra, Dinizia, Distemonanthus, Elizabetha, Eperua, Erythrophleum, Gleditschia, Goniorrhachis, Gossweilerodendron, Gymnocladus, Haematoxylon, Hardwickia, Heterostemon, Holocalyx, Humboldtia, Hymenaea, Hymenostegia, (Ibadja), Intsia, Isoberlinia, Kingiodendron, Koombassia, Lecointea, Libidibia, Loesenera, Macrobium, Martiodendron, Melanoxylon, Mezoneuron, Mildbraediodendron, Mora, Oxystigma, Pahudia, Parkinsonia, Peiranisia, Peltogyne, Peltophorum, Poeppigia, Poincianella, Prioria, Pseudocopaiva, Pterogyne, Pterygopodium, Recordoxylon, Saraca, Schizolobium, Schotia, Sciacassia, Sclerolobium, Sindora, Stahlia, Storckia, Tachigalia, Tamarindus, Trachylobium, Vouapa, Zollernia, Zuccagnia.

LITERATURE

(i) On General Anatomy

Dastur and Saxton 543, Friesner 720, George 755, 2522, Gilg and Schuster 780, Handa 885, 886, Levin 1366, Loeffler 1388, Maplethorpe 1437, Morvillez 1558, Planchon 1727, 1729, Russell 1971, Russell and Hédin 1974, Saber 1976, Sabnis 1977, Voigt 2339, Wagner 2343, Watari 2364, Zemke 2505.

(ii) On Wood Structure

Bailey 78, Becking *et al.* 164, Benoist 170, den Berger 179, 182, 183, Besson 186, B. Hond. Forestry Department 274, Brown, F. B. H. 280, Brown H. P. 289, Burgerstein 310, 312, Cooper and Record 461, Coster 481, Desch 568, 569, Dixon 592, Fanshawe 2519, Foxworthy 705, Handa 885, Howard 1088, Janssonius 1147, 1154, Jentsch 1176, Jones 1191, Kanehira 1206, 1209, Kramer 1275, Kribs 1283, Lecomte 1334, Martin-Levigne 1450, Ménaud 1492, Nicoloff 1593, Normand 1612, 1615, 1616, 1621, Pearson and Brown 1679, Pereira 1687, Pfeiffer, H. 1711, Pfeiffer, J. Ph. 1713, Record 1783, 1792, 1797, 1827, 1834, 1836, 1843, 1851, 1864, 1881, Record and Hess 1886, Record and Mell 1894, Riera 1937, Scott 2075, Stone 2202, 2206, 2207, Torres 2269, Wagner 2343, Wallis 2348.

115 C. PAPILIONACEAE

(FIG. 106 on p. 472; FIG. 112 on pp. 504 and 505; FIG. 113 on p. 508; FIG. 114 on p. 512; FIG. 115 on p. 520; FIG. 116 on p. 522; FIG. 117 on p. 526)

SUMMARY

(i) GENERAL

A large, widely distributed family, consisting of trees, shrubs, herbs, and including some xeromorphs. Although the family is well defined by its floral and fruit characters, there is a considerable range of anatomical variation which is largely correlated with the wide diversity of habit shown by the different genera and species. Other anatomical variations are xeromorphic in nature. Some anatomical characters are common to a very wide range of genera, but none of them are sufficiently distinctive to demarcate the Papilionaceae from all other families at a glance.

The **hairs** are of glandular and non-glandular types. The latter include typical, uniseriate hairs each with short basal cells accompanied by an elongated terminal cell. Other kinds of non-glandular hairs are two-armed, hooked, branched, and multicellular and shaggy. The glandular hairs may be club-shaped with long or short stalks; with specially large, spherical heads; uni- or biseriate but bulbous towards the base. The **epidermis** of the leaf is characterized by the common occurrence of angular folds in the anticlinal walls; by the development of papillae, especially in the lower surface, in a great number of genera; by being frequently mucilaginous. The arrangement of the cells surrounding the **stomata** is very variable, no one type being constant throughout a single tribe. The following are the main types. (a) Rubiaceous, accompanied on either side by 1 or 2 cells lying parallel to the ostiole. (b) Surrounded by a rosette of cells. (c) Cruciferous. (d) Ranunculaceous.

Secretory elements. Cells or sacs, with or without tanniniferous contents, often stained brown in herbarium specimens, and sometimes containing substances such as protein, mucilage, &c., are a very common feature both in the stem and leaf. Secretory cavities of various types also occur, whilst canals have been observed in *Derris* and *Myroxylon*. The **crystals**, which are predominantly solitary, but very variable in size and shape, sometimes have a characteristic appearance and distribution, especially in the leaf epidermis. Crystalliferous cells frequently form a sheath along the outer boundary of the pericyclic sclerenchyma. Amongst other cellular contents **indigo** is worthy of special mention, although it has been recorded from only a few genera. The **petiole** exhibits a considerable range of vascular structure, which appears to be partly correlated with the habit of the plant.

The **young stem** is frequently assimilatory in xeromorphic species. Leafy, wing-like expansions of the stem occur in certain genera, e.g. in *Lathyrus* spp. Palisade chlorenchyma is common in assimilatory stems. The assimilatory stems of *Cytisus*, *Genista*, *Spartium*, *Ulex*, and related genera have been the subject of several special investigations, whilst Dr. C. L. Hare, while working at Kew, has made numerous observations on stems which exhibit features of special interest (see 'Young Stem'). The position in which the **cork** originates is most variable, ranging from the sub-epidermis to the pericycle, considerable

differences being found between members of a single genus, or sometimes within a species. Cork cells typically thin-walled, but in woody genera such as *Cladrastis*, *Laburnum*, *Wistaria*, with thickened tangential walls; some layers of cork develop as typical stone cells in *Ulex europeus* Linn. The cork is replaced by **aerenchyma** in a few species and is not formed at all in some of the herbaceous members of the Loteae, Trifolieae, and Vicieae with assimilatory stems. The distribution of sclerenchyma in the **pericycle** is also very variable, as it may be in separate strands or in a composite and continuous ring. Pericyclic fibres often exhibit little lignification. Various types of stem structure have been recognized in herbaceous species, depending on the nature and position of the sclerenchyma in relation to the vascular bundles. Herbaceous species are typically provided with **vascular bundles** separated by conspicuous medullary rays, but in the woody ones the primary rays are usually narrow (see 'Young Stem' below). **Cortical vascular bundles** occur in a few species, especially amongst those with winged or grooved stems. Two types of **anomalous structure** have been recorded. In the first of these there are successive growth rings in the primary cortex, pericycle, or, more rarely, in the phloem. The second type, which is less common, consists in the development of interxylary phloem. The most noteworthy and familiar fact about the **root system** is the almost universal occurrence of nodules containing nitrogen-fixing bacteria.

(ii) Wood

Vessels. Radial multiples of 2 or 3 cells moderately common in most species; with an oblique or tangential pattern in several genera; ring-porous or semi-ring-porous in nearly a quarter of the genera; spiral thickening moderately common; perforations simple, intervascular pitting alternate and small, pits to parenchyma typically similar but simple or subtending larger pits in some species; pits vested; members moderately to very short. **Parenchyma** usually abundant and occasionally forming the ground tissue; most typically in either confluent or more regular bands, though aliform or vasicentric in several genera; diffuse strands present in only a few genera; terminal bands sometimes present; chambered crystals common on the margins of the banded or paratracheal parenchyma, typically with 8 and not more than 11 crystals per strand, but with more in a few genera; strands very commonly of 1-2 or only 1 cell (fusiform), storied in most of the genera. **Rays** 1-12 (mostly 2-3) cells wide (except for a few species with rays 20 or more cells wide), or exclusively uniseriate; some genera with narrow procumbent cells, but relatively fewer than in the Caesalpiniaceae; homogeneous in about 45 per cent. of the genera; with few uniseriates in about two-thirds of the genera with multiseriate rays; distinctly storied in genera with low rays, usually without echelon arrangement in the others, the rays being more than 1 story high. **Fibres** with small simple pits; very rarely septate; of medium length to very short. **Intercellular canals** of the vertical, scattered type present in one genus. **Included phloem** of the 'concentric' and 'disperse' types present in a few genera, mostly of the former type.

LEAF

Very variable in structure owing to the wide range of leaf types in the

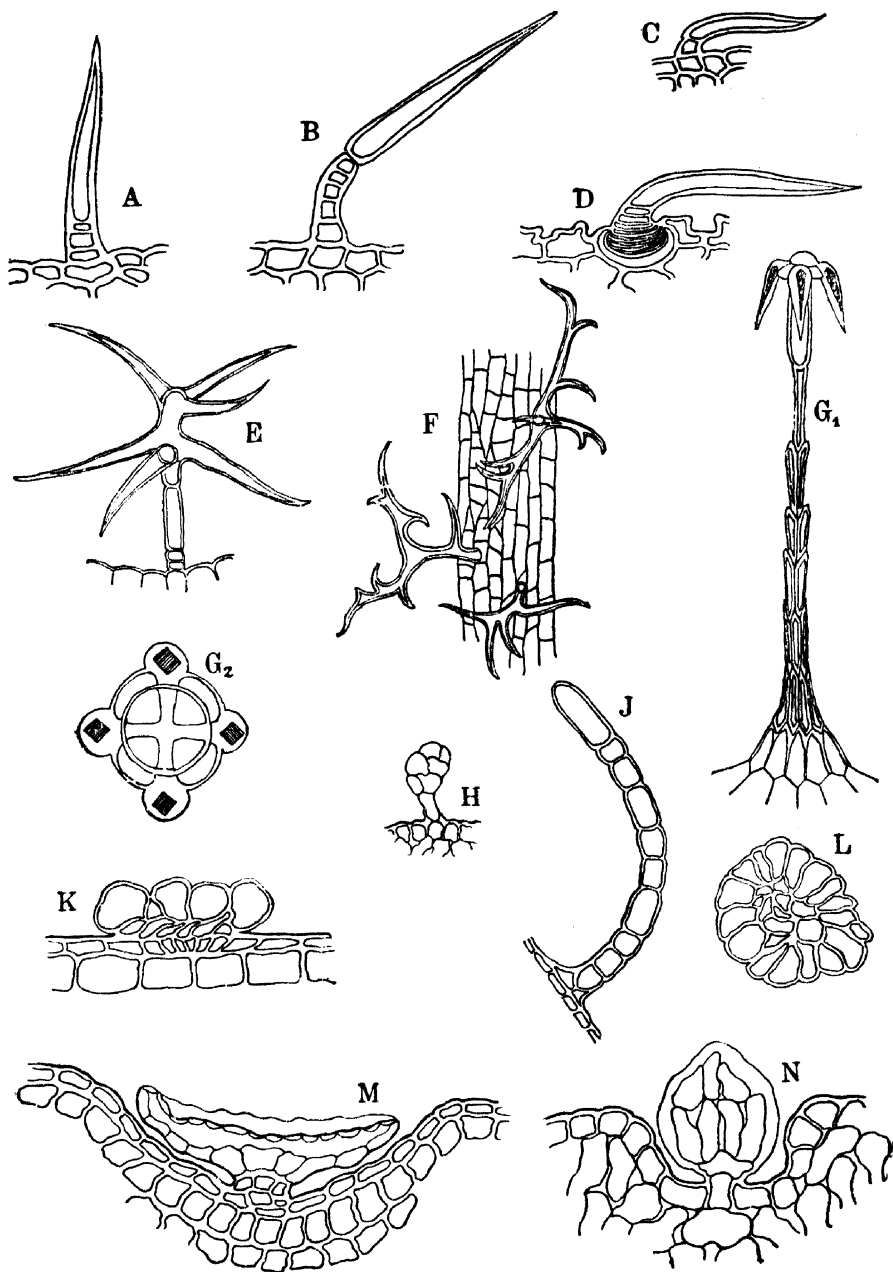


FIG. 112. LEGUMINOSAE—PAPILIONACEAE

A-C, Ordinary papilionaceous hairs. D, Simple hair of *Lonchocarpus negrensis* Benth., with bulbous septate base. E, Branched hair of *Erythrina indica* Lam. F, Branched trichomes of *Dipteryx rosea* Spruce. G₁, Anchor-like shaggy hair of *Cranocarpus martii* Benth.; G₂, Head of the anchor, seen from above. H, Glandular hair of the Phaseoleae. J, Uniseriate glandular hair of *Pongamia glabra* Vent. K-L, Peltate glands of *Pterocarpus ancylocalyx* Benth. M, Section through a peltate gland of *Centrolobium robustum* Mart. N, External gland of the Phaseoleae. O, Bulbous hair of *Fagelia*. P-Q, *Vicia faba* Linn.; P, Transverse section through a stipule with its glandular area; Q, The glands of the glandular area strongly magnified.—A, B, C, D, J, K, L and M after Köpf; H, N after Debolt; Q and R after Haberlandt; E, F, G₁, G₂ and O by Solereder.

family; usually dorsiventral and less frequently isobilateral. **Hairs** glandular and non-glandular.

I. *Non-glandular types* (Fig. 112 A-D)

- (a) Uniseriate, with a variable number of short basal cells, accompanied by an elongated terminal cell. This type particularly prevalent, according to Solereder, in the Dalbergieae, Galageae, Hedysareae, Phaseoleae, Sophoreae, and Swartzieae, and recorded also in the genera *Anagyris*, *Cytisus*, *Gastrolobium*, *Genista*, *Lotus*, *Lupinus*, *Podalyria*, *Retama*, *Trifolium*, *Ulex*, *Vicia*.

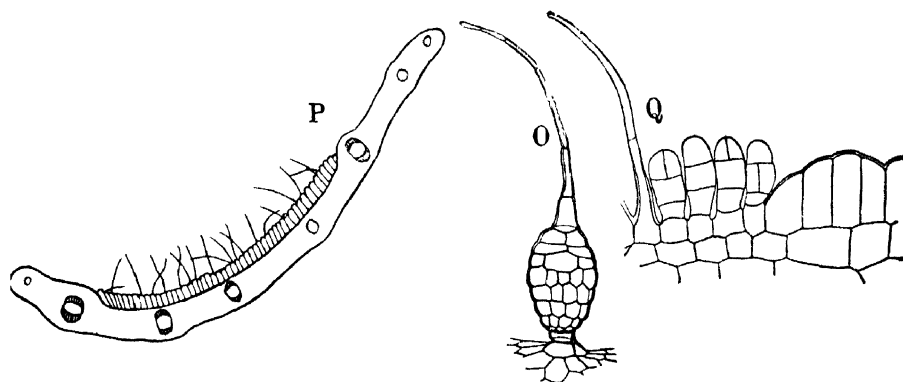


FIG. 112. (continued)

- (b) Uniseriate, consisting of cells of more equal size. This type infrequent, recorded, for example, in *Ononis*.
- (c) Equally or unequally two-armed in species of *Aspalathus*, *Astragalus*, *Buchenroedera*, *Calycotome*, *Chorizema*, *Crotalaria* (rare), *Cyamopsis*, *Dillwynia*, *Diplostropis*, *Erinacea*, *Erythrina*, *Genista* (rare), *Gueldenstaedtia*, *Hovea*, *Indigofera* (common), *Jacksonia*, *Lebeckia*, *Lessertia*, *Lotononis*, *Mirbelia*, *Oxylobium*, *Priestleya*, *Pultenaea*, *Sphaerophysa*, *Swainsona*.
- (d) Branched hairs: (i) with a uniseriate stalk in *Erythrina indica* Lam. (Fig. 112 E); (ii) unicellular in *Dipteryx* spp. (Fig. 112 F).
- (e) Hooked hairs, with short basal cells, and a larger bent, terminal cell in *Alysicarpus*, *Barbiera*, *Canavalia*, *Centrosema*, *Clitoria*, *Desmodium*, *Eleiotis*, *Leptodesmia*, *Lourea*, *Mecopus*, *Ougeinia*, *Periandra*, *Phaseolus*, *Pictetia*, *Pseudarthria*, *Psoralea* (terminal cell parallel to leaf surface), *Pycnospora*, *Uria*.
- (f) Multicellular, shaggy hairs recorded only in *Aeschynomene*, *Arachis*, *Chapmannia*, *Cranocarpus*, *Discolobium*, *Geissaspis*, *Ormocarpum*, *Smithia* (bottle-shaped), *Stylosanthes*. Anchor-like shaggy hairs occur in *Cranocarpus martii* Benth. (Fig. 112 G).
- (g) Stellate hairs recorded in *Erythrina*.

II. *Glandular types*

- (a) Club-shaped, with or without a distinct stalk, common in the Phaseoleae (Fig. 112 H), and in *Alysicarpus*, *Barbiera*, *Canavalia*, *Cicer* (long

stalked), *Chadsia*, *Desmodium*, *Eleiotis*, *Hallia*, *Hecastophyllum*, *Leptodesmia*, *Lonchocarpus*, *Lourea*, *Medicago* (long stalked in certain species), *Melilotus*, *Milletia*, *Mundulea*, *Olneya*, *Ononis* (long stalked), *Parochetus*, *Psoralea*, *Rhynchosia*, *Tephrosia*, *Trifolium*, *Trigonella*.

- (b) Peltate hairs of various types in species of *Brongniartia*, *Centrolobium* (Fig. 112 M), *Glycyrrhiza*, *Harpalyce*, *Petteria*, *Pterocarpus* (Fig. 112 K-L).
- (c) Especially large, spherical headed glands (Fig. 112 N) with a few short basal cells, the secretion being formed in abundance between the cuticle and cells of the head, in *Atylosia*, *Cajanus*, *Cylista*, *Dunbaria*, *Eriosema*, *Flemingia*, *Rhynchosia*.
- (d) Uni- or biseriate hairs, bulbous towards the base, recorded in *Adesmia*, *Atylosia*, *Eriosema*, *Fagelia* (Fig. 112 O), *Ormocarpum*, *Rhynchosia*.

Glandular leaf teeth in *Myroxylon pubescens* H. B. et K. **Extra-floral nectaries** on the stipules of *Canavalia*, *Dolichos*, *Erythrina* (on the spines also), *Vicia* (composed of stalked glands mixed with clothing hairs (Fig. 112 P-Q)).

Cuticle with verrucose thickenings, often surrounding peg-like projections of the cellulose membranes of the adjoining epidermal cells and thus producing the appearance of pseudo-pitting in *Aotus*, *Aspalathus*, *Burtonia*, *Cyclopia*, *Daviesia*, *Lupinus*, *Oxylobium*, *Podalyria*, *Pultenaea*. Cuticular projections, sometimes resembling papillae but at others more like hairs, recorded in species of *Aotus*, *Brachysema*, *Chorizema*, *Daviesia*, *Dillwynia*, *Eutaxia*, *Gastrolobium*, *Gompholobium*, *Mirbelia*, *Oxylobium*, *Pultenaea*, *Sphaerolobium*.

Epidermis. Anticlinal walls provided with angular folds in certain species of *Anagyris*, *Anthyllis*, *Coronilla*, *Dorycnium*, *Euchresta*, *Hippocrepis*, *Hosackia*, *Hymenocarpus*, *Lotus*, *Melilotus*, *Onobrychis*, *Ononis*, *Securigera*, *Trifolium*, *Trigonella*.

Lower epidermis papillose or sub-papillose in species of *Abrus*, *Adenocarpus*, *Alysicarpus*, *Amphicarpaea*, *Anthyllis*, *Aotus*, *Argyrolobium*, *Barbiera*, *Bossiaea*, *Bowdichia*, *Brachysema*, *Brongniartia*, *Burtonia* (with coronulate apices, the individual papillae connected by cuticular ridges), *Calpurnia*, *Calycotome*, *Camptosema*, *Chorizema*, *Cladrastis*, *Clitoria*, *Coelidium*, *Cytisus*, *Dalbergia*, *Dalea*, *Daviesia*, *Derris*, *Desmodium*, *Dillwynia* (in longitudinal rows), *Diphysa*, *Diplostropis*, *Discolobium*, *Dorycnium*, *Drepanocarpus*, *Eleiotis*, *Erythrina*, *Eutaxia*, *Gastrolobium*, *Genista*, *Glycine*, *Gompholobium*, *Goodia*, *Hardenbergia*, *Harpalyce*, *Hosackia*, *Hovea*, *Hypocalyptus*, *Indigofera*, *Kennedy*, *Laburnum*, *Latrobea*, *Leptodesmia*, *Lespedeza*, *Liparia*, *Lonchocarpus*, *Lotus*, *Lourea*, *Lupinus*, *Machaerium*, *Mecopus*, *Mirbelia*, *Mucuna*, *Muelleria*, *Myrosporum*, *Ougeinia*, *Oxylobium*, *Periandra*, *Phyllota*, *Piscidia*, *Poitea*, *Priestleya*, *Priotropis*, *Pseudarthria*, *Pterocarpus*, *Pterodon*, *Pueraria*, *Pultenaea*, *Pycnospora*, *Rhynchosia*, *Robinia*, *Shuteria*, *Sophora*, *Sphaerolobium*, *Strongylodon*, *Swartzia*, *Sweetia*, *Templetonia*, *Trifolium*, *Uraria*.

Papillose upper epidermis recorded only in species of *Dalbergia* and *Spartium*.

Epidermis often including a proportion of mucilaginous cells in species of *Adenocarpus*, *Adesmia*, *Aeschynomene*, *Ammodendron*, *Amorpha*, *Andira*, *Aotus*, *Arachis*, *Argyrolobium*, *Aspalanthus*, *Atylosia*, *Borbonia*, *Bossiaea*, *Bowdichia*,

Brachysema, *Brongniartia*, *Burtonia*, *Calycotome*, *Camptosema*, *Canavalia*, *Chaetocalyx*, *Chapmannia*, *Chorizema*, *Cladrastis*, *Clitoria*, *Cratylia*, *Crotalaria*, *Cyclopia*, *Cymbosema*, *Cytisus*, *Dalbergia*, *Dalea*, *Dichilus*, *Dillwynia*, *Dioclea*, *Diphysa*, *Discolobium*, *Dolichos*, *Drepanocarpus*, *Erinacea*, *Eriosema*, *Euchlora*, *Eutaxia*, *Galactia*, *Gastrolobium*, *Geissaspis*, *Genista*, *Goodia*, *Hermimera*, *Heylandia*, *Hovea*, *Kennedya*, *Laburnum*, *Latrobea*, *Lebeckia*, *Lotononis*, *Melolobium*, *Mirbelia*, *Nissolia*, *Ormocarpum*, *Oxylobium*, *Periandra*, *Petalostemon*, *Petteria*, *Phaseolus*, *Phyllota*, *Pictetia*, *Piscidia*, *Platymiscium*, *Platypodium*, *Poecilanthus*, *Poiretia*, *Priotropis*, *Pterocarpus*, *Pultenaea*, *Rafnia*, *Rhynchosia*, *Rothia*, *Rudolphia*, *Smithia*, *Soemmeringia*, *Sophora*, *Spartium*, *Sphaerolobium*, *Strongylodon*, *Stylosanthes*, *Swartzia*, *Sweetia*, *Templetonia*, *Tephrosia*, *Ulex*, *Viborgia*, *Viminaria*, *Zornia*.

Epidermal cells with gelatinous inner membranes not recorded from the Loteae, Trifolieae, and Vicieae.

Epidermal cells vertically divided by thin walls in species of *Andira*, *Centrolobium*, *Cytisus*, *Dalbergia*, *Dipteryx*, *Geoffraea*, *Hecastophyllum*, *Petteria* (near the stomata), *Platypodium*, *Poecilanthus*, *Pterodon*. Upper epidermal cells specially large in *Argyrolobium emirense* Baker (Lacoste 1312).

Hypoderm present on the upper side of the leaf in species of *Andira*, *Canavalia*, *Cratylia*, *Crotalaria*, *Dalbergia*, *Diplotropis*, *Hecastophyllum*, *Lonchocarpus*, *Myrospermum*, *Myroxylon*, *Sophora*, *Zollernia*; on the lower side in a few species of *Andira*, *Bowdichia*, *Centrolobium*, *Dillwynia*, *Eutaxia*, *Geoffraea*, *Pterocarpus*, *Pultenaea*, *Swartzia*, *Sweetia*; beneath both surfaces in species of *Daviesia* and *Pterocarpus*.

Stomata very variable, no single type being present throughout any one of the tribes, nor is the distribution constant throughout many of the genera. Present on both surfaces in all investigated Loteae and Trifolieae as well as in species of *Alysicarpus*, *Arachis*, *Argyrolobium*, *Canavalia*, *Crotalaria* (pro parte), *Dalbergia*, *Desmodium* (pro parte), *Dolichos*, *Eriosema*, *Indigofera*, *Mucuna* (pro parte), *Mundulea* (very small in some species), *Psophocarpus*, *Rhynchosia*, *Sesbania*, *Smithia*, *Strongylodon*, *Vigna*, *Voandzeia*, *Zornia*. Often confined to the upper surface in *Coelidium*, *Dillwynia*, *Diphaca*, *Eutaxia*, *Geoffraea*, *Pultenaea*; confined to the lower surface in *Aeschynomene*, *Chadsia*, *Clitoria*, *Crotalaria* (pro parte), *Derris*, *Desmodium* (pro parte), *Dioclea*, *Dumasia*, *Fagelia*, *Leptodesmia*, *Lonchocarpus*, *Milletia*, *Mucuna* (pro parte), *Strongylodon*; parallel to one another but placed transversely to the direction of the midrib or of the longitudinal axis of assimilating branches of *Alhagi*, *Anarthrophyllum*, *Carmichaelia*, *Daviesia*, *Latrobea*.

Arrangement of surrounding cells as follows.

- (a) Rubiaceous in *Alysicarpus*, *Arachis*, *Bowdichia*, *Cicer* (some of the stomata), *Cranocarpus*, *Dalbergia* (most stomata), *Dalhousiea*, *Desmodium*, *Dillwynia*, *Diplotropis*, *Eleiotis*, *Eutaxia*, *Geissaspis*, *Hallia*, *Hovea*, *Hypocalyptus*, *Jacksonia*, *Lathyrus* (some stomata), *Lens* (some stomata), *Leptodesmia*, *Lespedeza*, *Lourea*, *Mecopus*, *Milletia*, *Ononis*, *Ormosia*, *Ougeinia*, the Phaseoleae, *Pseudarthria*, *Psoralea*, *Pycnospora*, the Swartzieae (except *Zollernia*), *Uraria*, *Vicia* (some stomata).
- (b) Rubiaceous but with 2 pairs of subsidiary cells parallel to the pore in species of *Aotus*, *Brachysema*, *Dillwynia*, *Oxylobium*.

- (c) Surrounded by 3 or more subsidiary cells in most Galageae, Hedysareae, Podalyrieae and Sophoreae, and sometimes in *Abrus*, *Crotalaria* (Lacoste 1311), *Euchresta*, *Gastrolobium*, *Jacksonia*, *Latrobea*, *Pterocarpus*, *Pultenaea*, *Scorpiurus*, and *Sphaerolobium*.
- (d) Approximating to the cruciferous type in species of *Borbonia*, *Crotalaria*, *Lebeckia*, *Lotononis*, *Priotropis*, *Rafnia*, *Viborgia*.
- (e) Surrounded by a rosette of cells in species of *Anarthrophyllum*, *Genista*, *Lebeckia*, *Templetonia*.

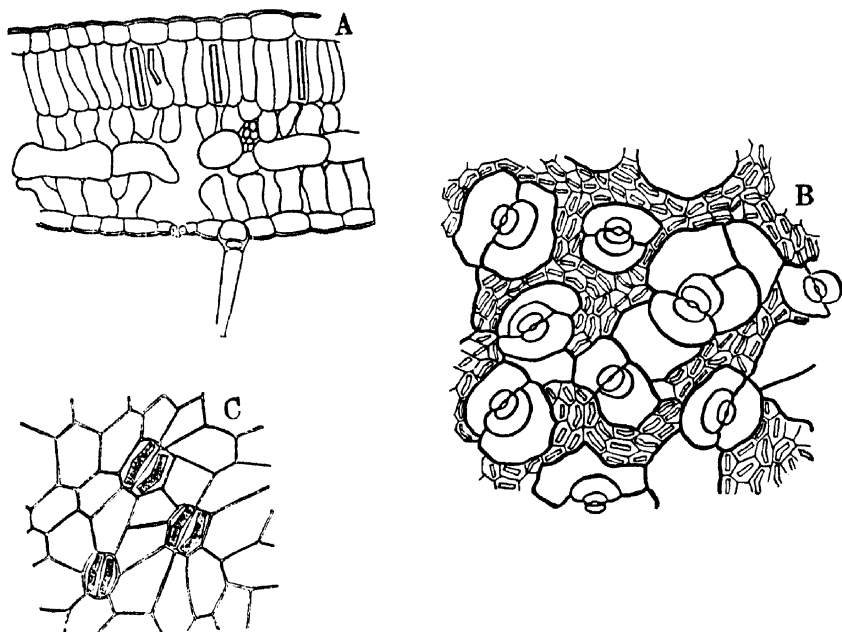


FIG. 113. LEGUMINOSAE—PAPILIONACEAE

A, Transverse section of the leaf of *Rhynchosia rufescens* DC. with styloid-like crystals in the palisade-tissue. B, Surface-view of the epidermis of the leaf of *Stylosanthes procumbens* Sw. C, Twin crystal-containing cells in the epidermis of the leaf of *Canavalia villosa* Benth.—By Solereder.

- (f) Ranunculaceous in most Loteae and Vicieae (for *Vicia* see also (a) above).
- (g) Special type in *Stylosanthes* (Fig. 113 B).

Central layers of **mesophyll** occupied by cells containing little chlorophyll, and often, but not invariably, filled with tanniniferous contents which are coloured brown in dried material in species of *Alysicarpus*, *Arachis*, *Butea*, *Calopogonium*, *Camptosema*, *Cajanus*, *Canavalia*, *Chapmannia*, *Cleobulia*, *Cranocarpus*, *Cratylia*, *Cylista*, *Cymbosema*, *Derris*, *Desmodium*, *Dioclea*, *Dolichos*, *Dunbaria*, *Eleiotis*, *Eriosema*, *Erythrina*, *Fagelia*, *Flemingia*, *Galactia*, *Glycine*, *Halimodendron*, *Hardenbergia*, *Indigofera*, *Kennedya*, *Leptodesmia*, *Lespedeza*, *Lonchocarpus*, *Muelleria*, *Mundulea*, *Ougeinia*, *Periandra*, *Petalostemon*, *Phaseolus*, *Physostigma*, *Pongamia*, *Pseudarthria*, *Pueraria*, *Pycnospora*, *Rhynchosia*, *Rudolphia*, *Spatholobus*, *Stylosanthes*, *Tephrosia*, *Teramnis*; aqueous tissue recorded in the corresponding position in species of *Alysicarpus*,

Crotalaria, *Psoralea* (Sabnis 1977). Fibres or branched **sclerenchymatous idioblasts** present in the mesophyll of a few species of *Ammodendron*, *Andira*, *Bossiaea*, *Bowdichia*, *Dillwynia*, *Ormosia*, *Platymiscium*, *Pultenaea*, *Swartzia*. Sclerosed parenchyma recorded in the mesophyll of *Buchenroedera*.

Veins variable in structure, with or without a sheath of sclerenchyma; smaller ones embedded or vertically transcurrent, the latter type recorded particularly in certain Genisteae, Podalyriaceae, Trifolieae, and Viciaceae, as well as in species of *Alysicarpus*, *Chadsia*, *Rhynchosia*, *Tephrosia*. Median veins containing two opposite systems of bundles, with their xylem groups abutting on one another in those species of *Daviesia* having approximately horizontal leaves. An annular arrangement of bundles surrounding a pith-like tissue at the centre of the leaves occurs in certain species of *Lebeckia*.

Petiole. Structure very variable, differences being correlated to some extent with the general morphology of the leaf and the habit of the plant. Some idea of the range of structure is indicated by the following information concerning the appearance of transverse sections through the distal end of the petioles represented in the slide collection at Kew. For recent detailed descriptions of the vascular system throughout the length of the petiole the work of Morvillez (1560) and Watari (2364) should be consulted.

I. Main vascular strand composed of separate bundles.

- (a) In the form of a widely open arc in *Arachis hypogaea* Linn., *Coronilla vaginalis* Lam., *Lotus tetragonolobus* Linn., *Medicago sativa* Linn. (3 bundles only), *Melilotus officinalis* (L.) Lam., *Trifolium ochroleucum* Huds.
- (b) U-shaped, but ends not incurved in *Baptisia australis* R. Br., *Cicer arietinum* Linn., *Colutea persica* Boiss., *Lathyrus pratensis* Linn., *L. sylvestris* Linn. (wings well developed), *Lespedeza formosa* Koehne, *Vicia cracca* Linn.
- (c) U-shaped but with incurved ends in *Astragalus frigidus* A. Gray (Fig. 114 c), *Chorizema cordatum* Lindl., *Colutea arborescens* Linn., *Psoralea onobrychis* Nutt.
- (d) U-shaped with incurved ends and dorsiventrally compressed in *Caragana microphylla* Lam., *Vicia gigantea* Bunge.
- (e) Cylindrical and approximately circular in *Caragana arborescens* Lam., *Chadsia* (Dubard & Dop 611), '*Crotalaria axillaris* Hort.' (according to Lacoste (1311) cylindrical and arc-shaped strands occur in different species of *Crotalaria*), *Erythrina crista-galli* Linn., *Galega officinalis* Linn. (surrounding a hollow pith), *Glycine soja* Sieb. et Zucc., *Glycyrrhiza glabra* Linn., *Halimodendron halodendron* Druce, *Lathyrus maritimus* Bigel (Fig. 114 g), *Lupinus mutabilis* Sweet (pith hollow), *Phaseolus multiflorus* Willd., *Pisum elatius* Bieb., *Robinia pseudacacia* Linn., *Wistaria floribunda* DC., *W. sinensis* Sweet.
- (f) Cylindrical but dorsally concave in *Apios tuberosa* Moench.

II. Main vascular strand continuous, i.e. consisting of a single vascular strand.

- (a) U-shaped, but ends not incurved in *Spartium junceum* Linn. and *Thermopsis montana* Nutt.
- (b) U-shaped, but dorsally compressed and with strongly incurved ends in *Indigofera gerardiana* R. Grah. (according to Lacoste (1312) the petiole structure varies considerably in different species of *Indigofera*),

Myroxylon balsamum (L.) Harms var. *pereirae* (Royle) Harms (Fig. 114 B), *Petteria ramentacea* Prsl., *Piptanthus tomentosus* Franch, *Sophora viciifolia* Hance.

- (c) Cylindrical and approximately circular in *Abrus precatorius* Linn. (de Boer 214), *Castanospermum australe* A. Cunn., *Cladrastis sinensis* Hemsl., *C. tinctoria* Rafin, *Derris malaccensis* Prain (Fig. 114 A), *Laburnum alpinum* Bercht et Prsl., *L. anagyroides* Med., *Lonchocarpus sericeus* H. B. et K., *Robinia viscosa* Vent., *Sophora japonica* Linn.

Accessory bundles observed in the wings or 'cortex' in the same species of *Apios*, *Castanospermum*, *Derris*, *Glycine*, *Glycyrrhiza*, *Indigofera*, *Laburnum*, *Lathyrus*, *Lespedeza*, *Lonchocarpus*, *Myroxylon*, *Phaseolus*, *Piptanthus*, *Robinia*, *Sophora*, *Vicia*, *Wistaria*. Pericyclic fibres usually present around the main vascular strand, but none observed in *Chorizema*, *Glycine*, *Melilotus*, *Phaseolus*, *Spartium*, *Thermopsis*.

Petioles whose vascular structure does not conform to any of the above types include the following. *Desmodium gyrans* DC. with a triangular petiole with a single bundle in each of the three angles. *Platyosprion platycarpum* Maxim. with a cylindrical but dorsally concave vascular strand having a small accessory bundle in the concavity. *Mucuna pruriens* DC. with a flattened petiole supplied by a compressed circle of widely spaced vascular bundles (Lacoste 1915). Small secretory canals observed in the outer cortical region of the petiole in *Derris malaccensis*, and larger ones in *Myroxylon balsamum* var. *pereirae*.

Secretory elements (see also 'Axis'). Cells or sacs containing tannin, protein, or a gum-like substance, often coloured brown in dried material, observed or recorded in various parts of the mesophyll or petiole in species of the following genera, but probably present in many others as well, *Alhagi*, *Anthyllis*, *Aotus*, *Apios*, *Brachysema*, *Calophaca*, *Caragana*, *Castanospermum*, *Chorizema*, *Cladrastis*, *Coronilla*, *Corynella*, *Cyclopia*, *Cytisopsis*, *Dalbergia*, *Daviesia*, *Derris*, *Desmodium*, *Dillwynia*, *Diphaca*, *Dorycnium*, *Ebenus*, *Erythrina*, *Eutaxia*, *Eversmannia*, *Glycine*, *Glycyrrhiza*, *Goodia*, *Hallia*, *Halimodendron*, *Hedysarum*, *Helminthocarpum*, *Hosackia*, *Indigofera* (very numerous in some species), *Latrobea*, *Lespedeza*, *Lonchocarpus*, *Lotus*, *Machaerium* (flask shaped, belonging to the epidermis but penetrating into the mesophyll), *Melilotus*, *Mirbelia*, *Muelleria*, *Mundulea*, *Myroxylon*, *Olneya*, *Onobrychis*, *Ormocarpum*, *Ornithopus*, *Oxylobium*, *Parochetus*, *Petalostemon*, *Phaseolus*, *Phyllota*, *Poitea*, *Pongamia*, *Psoralea*, *Pterocarpus*, *Pultenaea*, *Rhynchosia*, *Robinia*, *Sabinea*, *Scorpiurus*, *Sophora* (often flask shaped as in *Machaerium*), *Taverniera*, *Tephrosia*, *Wistaria*.

Secretory cavities of various types, such as those shown in Fig. 106 C, usually appearing as transparent dots, recorded in *Amicia*, *Amorpha*, *Anthyllis* (with bright yellow contents), *Apoplanesia*, *Dalea*, *Derris*, *Dipteryx*, *Eysenhardtia*, *Lonchocarpus*, *Marina*, *Milletia*, *Muelleria*, *Myrospermum*, *Myroxylon*, *Petalostemon*, *Piscidia*, *Poiretia*, *Pongamia*, *Psoralea*, *Zornia*. Secretory canals observed in the petiole of *Derris malaccensis*.

Crystals mostly solitary, particularly in the Loteae and Trifolieae, occurring in the form of rhombohedra (especially accompanying the vascular bundles of the veins) or styloids (Fig. 113 A), the latter being more characteristic of

the mesophyll or epidermis. Spherical crystals observed only in *Dalea* and *Discolobium*; small crystalline grains or prisms recorded in the mesophyll of *Dalbergia*, *Derris*, *Haematophyllum*, *Swartzia*, *Virgilia*. Large rhombohedral or rod-shaped crystals, sometimes accompanied by small prismatic or acicular forms, are particularly characteristic of Australian species of Podalyriaceae; but crystals stated to occur exclusively in the form of small prisms or needles in species of *Cyclopia* and *Podalyria* endemic to S. Africa, as well as in species of *Anagyris*, *Baptisia*, *Piptanthus*, and *Thermopsis* from the northern hemisphere. Large crystals also recorded in *Bossiaea*, *Goodia*, *Hovea*, *Platylobium*, and *Templetonia*, and small cubes, prisms, or needles in *Adenocarpus*, *Amphithalea*, *Anarthrophyllum*, *Argyrolobium*, *Aspalathus*, *Borbonia*, *Calycotome*, *Coelidium*, *Crotalaria*, *Cytisus*, *Genista*, *Hypocalyptus*, *Lathriogyna*, *Lebeckia*, *Liparia*, *Lupinus*, *Melobium*, *Petteria*, *Priotropis*, *Spartium*, *Ulex*, *Viborgia*.

Rod-shaped crystals (styloids) recorded in the palisade tissue of *Abrus*, *Aeschynomene*, *Amphicarpea*, *Anthyllis*, *Arachis*, *Atylosia*, *Bossiaea*, *Calopogonium*, *Canavalia*, *Centrosema*, *Chapmannia*, *Clitoria*, *Cologania*, *Coronilla*, *Coursetia*, *Cytisopsis*, *Dalbergia*, *Dalea*, *Daviesia*, *Derris*, *Desmodium*, *Dioclea*, *Diphysa*, *Drepanocarpus*, *Eriosema*, *Erythrina*, *Eutaxia*, *Eysenhardtia*, *Flemingia*, *Galactia*, *Geoffraea*, *Glycine*, *Grona*, *Hammatolobium*, *Herminiera*, *Hovea*, *Indigofera*, *Isotropis*, *Lathyrus*, *Latrobea*, *Lonchocarpus*, *Lotus*, *Lourea*, *Machaerium*, *Milletia*, *Mucuna*, *Muelleria*, *Olneya*, *Ononis*, *Orobis*, *Pachyrhizus*, *Petalostemon*, *Petteria*, *Phaseolus*, *Pictetia*, *Platylobium*, *Poecilanthe*, *Poiteaea*, *Pongamia*, *Psoralea*, *Pueraria*, *Pultenaea*, *Rhynchosia*, *Robinia*, *Rudolphia*, *Sophora*, *Spatholobus*, *Strongylodon*, *Swartzia*, *Templetonia*, *Tephrosia*, *Teramnus*, *Trifolium* (a few species), *Vicia*, *Vigna*.

Various, and sometimes characteristically arranged, rod-shaped crystals occur in the epidermis of certain species of *Abrus*, *Arachis*, *Canavalia* (in isolated pairs of epidermal cells, Fig. 113 C), *Chapmannia*, *Cleobulia*, *Crano-carpus*, *Cratylia*, *Dalea*, *Dioclea*, *Dolichos*, *Drepanocarpus*, *Eriosema*, *Erythrina*, *Galactia*, *Geoffraea*, *Glycine*, *Milletia*, *Petalostemon*, *Psoralea*, *Rudolphia*, *Sophora*, *Stylosanthes* (curious distribution shown in Fig. 113 B), *Swartzia*.

Especially large crystals accompany the veins in *Brongniartia*, *Harpalyce*, and *Sabinea*. Large prismatic crystals, occupy the whole lumen of palisade-like cells immediately below the two-armed hairs in *Indigofera lespedezioides* H. B. et K. **Sphaero-crystalline masses** of unknown chemical composition, recorded in the epidermis, particularly in herbarium material, of *Anagyris*, *Argyrolobium*, *Aspalathus*, *Chorizema*, *Crotalaria*, *Cyclopia*, *Dillwynia*, *Eutaxia*, *Hovea*, *Latrobea*, *Phyllota*, *Piptanthus*, *Podalyria*, *Pultenaea*, *Thermopsis*.

Saponin in shapeless masses, stated to occur in the epidermis of *Aspalathus*. **Indigo**, or bodies resembling this substance, recorded in *Crotalaria*, *Helminthocarpus*, *Hosackia*, *Hymenocarpus*, *Indigofera*, *Lathyrus*, *Lens*, *Lotus*, *Melobium*, *Petalostemon*, *Priotropis*. For further details concerning the leaf structure in numerous species see Leupin's (1934) thesis.

AXIS

YOUNG STEM (Fig. 114 D, E, F, H, and I)

Epidermis of *Chorizema cordatum* Lindl. persistent, with very thick cuticle.

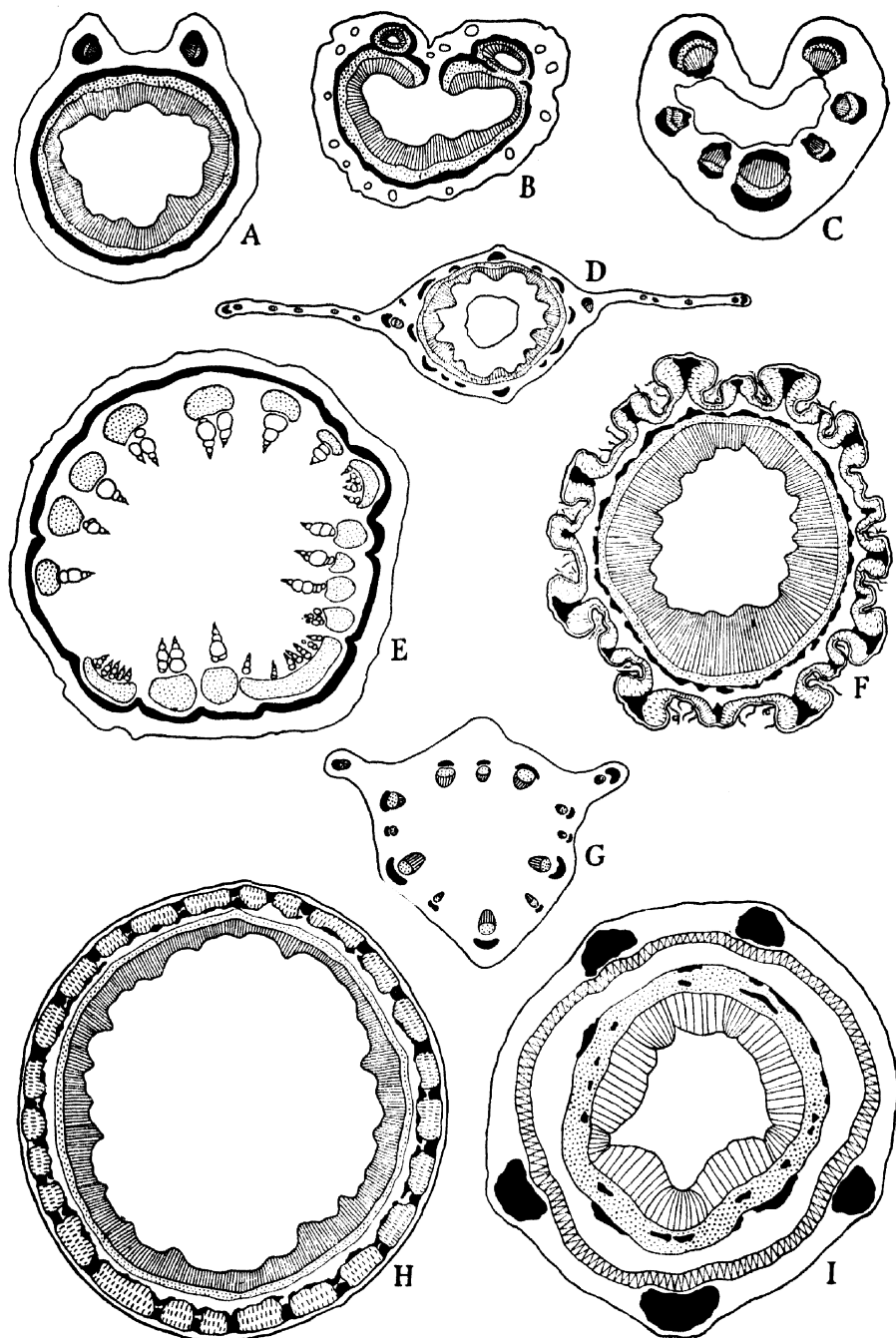


FIG. 114. LEGUMINOSAE—PAPILIONACEAE

A, *Derris malaccensis* Prain. Petiole $\times 18$. B, *Myroxylon balsamum* (L.) Harms var. *perirae* (Royle) Harms. Petiole $\times 18$. C, *Astragalus frigidus* A. Gray. Petiole $\times 18$. D, *Lathyrus sylvestris* Linn. Stem $\times 7$. E, *Apios tuberosa* Moench. Young Stem $\times 33$. F, *Cytisus albus* Link. Stem $\times 18$. G, *Lathyrus maritimus* Bigel. Petiole $\times 13$. H, *Spartium junceum* Linn. Stem $\times 18$. I, *Caragana arbore-scens* Lam. Young stem $\times 33$.

Cork arising in very varying positions, even amongst different members of a single genus.

- (a) Arising in the epidermis in *Abrus*, *Coursetia*, *Cytisus*, *Erinacea*, *Indigofera* (pro parte), *Loddigesia*, *Mundulea*, *Myroxyton*, *Oxylobium*, *Platyosprion*, *Pseudarthria*, *Pycnospora*, *Robinia*, *Ulex*, *Uraria*, *Virgilia*.
- (b) Arising in the sub-epidermis or between this and the sixth cell layer in species of *Aeschynomene*, *Amorpha*, *Amphitalea*, *Argyrolobium*, *Baphia*, *Buchenroedera*, *Calopogonium*, *Calycotome*, *Canavalia*, *Centrolobium*, *Centrosema*, *Chadsia*, *Coelidium*, *Cordyla*, *Coronilla*, *Cranocarpus*, *Cratylia*, *Cytisus*, *Dalbergia*, *Dalea*, *Desmodium*, *Dillwynia*, *Diphysa*, *Eutaxia*, *Eysenhardtia*, *Gastrolobium*, *Geissaspis*, *Geoffraea*, *Goodia*, *Hallia*, *Hovea*, *Hypocalyptus*, *Indigofera* (pro parte), *Laburnum*, *Lathriogyna*, *Liparia*, *Lotononis*, *Phaseolus*, *Pictetia*, *Podalyria*, *Priestleya*, *Priotropis*, *Pterocarpus*, *Pueraria*, *Pultenaea*, *Robinia*, *Sabinea*, *Smithia*, *Soemmeringia*, *Sophora*, *Spartium*, *Stylosanthes*, *Thermopsis*, *Wistaria*.
- (c) Arising in the middle of the cortex in *Anagyris*, *Atylosia*, *Camptosema*, *Cleobulia*, *Clitoria*, *Cylista*, *Dalhousiea*, *Eriosema*, *Erythrina*, *Galactia*, *Indigofera*, *Piptanthus*, *Psoralea*, *Rhynchosia*, *Rudolphia*.
- (d) Arising in the innermost layer of cortex in species of *Cicer*, *Colutea*, *Dioclea*, *Galega*, *Glycine*, *Halimodendron* (mucilaginous cork), *Lotus*, *Trifolium*.
- (e) Arising in positions varying from the middle of the cortex to the endodermis in species of *Hippocrepis*, *Lathyrus*, *Medicago*, *Onobrychis*, *Ononis*, *Orobis*.
- (f) Arising internally to the groups of pericyclic fibres in *Adenocarpus*, *Adesmia*, *Aspalathus*, *Borbonia*, *Colutea*, *Cytisus*, *Halimodendron*, *Lebeckia*, *Petteria*, *Sphaerophysa*, *Ulex*, *Viborgia*.

Aerenchyma is formed instead of cork in *Lotus uliginosus* Schkuhr, *Sesbania aculeata* Poir., and *S. marginata* Benth., and is stated to occur also in *Phaseolus* when grown in water cultures.

Outer part of the primary **cortex** often collenchymatous and containing stone cells. A large part of the cortex, in species with reduced leaves, composed of chlorenchyma, frequently exhibiting palisade structure and accompanied by abundant **stomata**, the latter sometimes restricted to grooves. Species with reduced leaves also frequently characterized by strands of fibres in the cortex or attached to the vascular system. In the old stems the cortical fibres may become exfoliated by a deep-seated phellogen, e.g. in the prominently ribbed stem of *Caragana arborescens* Lam. See also 'Stems with special features' on p. 516.

Pericycle containing either isolated strands of fibres or a composite and continuous ring of sclerenchyma.

- (a) Isolated strands of fibres, occasionally with stone cells between them, stated to occur in most Hedysareae and in at least certain species of *Adenocarpus*, *Alysicarpus*, *Ammodendron*, *Amphithalea*, *Anagyris*, *Apios*, *Arachis*, *Argyrolobium*, *Aspalathus*, *Astragalus*, *Baphia*, *Baptisia*, *Brongniartia*, *Buchenroedera*, *Calpurnia*, *Calycotome*, *Caragana*, *Carmichaelia*, *Chadsia* (pro parte), *Chorizema*, *Cicer*, *Cladrastis*, *Coelidium*, *Corynella*,

Courestia, *Crotalaria* (sometimes), *Cyclopia*, *Dalbergia*, *Dalea*, *Desmodium* (several species), *Dichilus*, *Dillwynia*, *Diphaca*, *Diphysa*, *Dolichos* (pro parte), *Drepanocarpus*, *Dumasia*, *Erinacea*, *Euchlora*, *Euchresta*, *Eutaxia*, *Eysenhardtia*, *Gastrolobium*, *Genista*, *Geoffraea*, *Goodia*, *Hali-modendron*, *Hecastophyllum*, *Hypocalyptus*, *Indigofera*, *Laburnum*, *Lathriogyna*, *Latrobea*, *Lebeckia*, *Lessertia*, *Loddigesia*, *Lotononis*, *Lupinus*, *Machaerium*, *Melolobium*, *Mirbelia*, *Mundulea* (pro parte), *Oxylobium*, *Petalostemon*, *Petteria*, *Piptanthus*, *Platymiscium*, *Platypodium*, *Podalyria*, *Poecilanthe*, *Priotropis*, *Psoralea*, *Pterocarpus*, *Rafnia*, *Rhynchosia* (pro parte), *Rothia*, *Sabinea*, *Sesbania* (pro parte), *Smithia*, *Sophora* (fibre groups becoming crescent shaped and almost continuous in '*S. flavescens* Hort' (Schilling 2032)), *Spartium*, *Sphaerophysa*, *Strongylodon*, *Tephrosia*, *Teramnus*, *Thermopsis*, *Tipuana*, *Ulex*, *Viborgia*, *Vigna*, *Zornia*.

- (b) A ring of fibres present in *Colutea* (pro parte), *Desmodium* (pro parte), *Galega*, *Glycyrrhiza*, *Harpalyce*.
- (c) A composite and continuous ring of sclerenchyma occurs in most of the Phaseoleae and in *Abrus*, *Aldina*, *Amorpha*, *Andira*, *Barbiera*, *Borbonia* (almost continuous), *Bowdichia*, *Brachysema*, *Calophaca*, *Canavalia*, *Centrolobium*, *Chadsia* (pro parte), *Cladrastis sinensis* (bounded externally by a sheath of cells containing large, solitary crystals), *Colutea* (pro parte), *Crotalaria* (pro parte), *Dalhousiea*, *Derris*, *Dioclea*, *Diploptropis*, *Dipteryx*, *Dolichos* (pro parte), *Eriosema*, *Fagelia*, *Glycine*, *Hovea*, *Leptodesmia*, *Liparia*, *Lonchocarpus*, *Millettia*, *Muelleria*, *Mundulea* (pro parte), *Myrosporum*, *Myroxylon*, *Olneya*, *Ormosia*, *Ougeinia*, *Piscidia*, *Platylobium*, *Pongamia*, *Priestleya*, *Pterodon*, *Pultenaea*, *Rhynchosia* (pro parte), *Robinia*, *Sesbania* (pro parte), *Swartzia*, *Sweetia*, *Virgilia*, *Voandzeia*, *Wistaria*, *Xanthocercis*, *Zollernia*.

Secondary **phloem** containing compact, sometimes stratified, strands of fibres, the latter occasionally exhibiting a mucilaginous layer. Chambered fibres containing rhombohedral crystals or styloids sometimes present as well. Medullary rays, where passing through the phloem, usually more than 4 cells wide, never sclerosed, broadened towards the exterior.

Vascular bundles in herbaceous species usually individually distinct in transverse sections, but exhibiting considerable differences in the nature of the interfascicular tissue. Some of the arrangements are as follows.

- (a) The groups of fibres belonging to each of the separate vascular bundles are connected to one another by sclerenchymatous parenchyma in most species of *Trifolium*.
- (b) Separate bundles united by sclerenchymatous parenchyma situated on the inside of the cambium in species of *Coronilla*, *Onobrychis*, *Ornithopus*, *Scorpiurus*, *Securigera*.
- (c) As (b), but prosenchymatous elements present amongst the sclerenchymatous parenchyma in species of *Astragalus*, *Astrolobium*, *Biserrula*, *Coronilla*, *Galega*, *Hippocrepis*, *Lotus*, *Medicago*, *Melilotus*, *Ononis*, *Phaca*, *Tetragonolobus*, *Trigonella*.
- (d) Interfascicular tissue on the inside of the cambium wholly sclerenchymatous in *Dorycnium*.

Xylem generally constituting a closed cylinder in woody genera and species; with or without distinct growth rings. Vessels frequently blocked with a dense black secretion in *Arachis hypogaea* Linn. and *Derris malaccensis* Prain.

Cortical vascular bundles present in species of *Borbonia*, *Bossiaea*, *Cytisus*, *Derris*, *Genista*, *Lathyrus*, *Mucuna*, *Orobis*, *Pisum*, *Retama*, *Strongylodon*, *Viborgia*, *Vicia*, especially in winged or grooved stems.

Secretory elements. (a) Tanniniferous cells, coloured brown in dried material, and sometimes containing protein, mucilage, and other materials as well, often in groups situated at the margin of the pith, in the primary or secondary phloem, or, more rarely, in the primary cortex.

- (i) In the pith and phloem in species of *Amorpha*, *Amphicarpaea*, *Apios*, *Atylosia*, *Butea*, *Cajanus*, *Calopogonium*, *Camptosema*, *Canavalia*, *Centrosema*, *Cleobulia*, *Clitoria*, *Cochlianthus*, *Cologetia*, *Cratylia*, *Cylista*, *Cymbosema*, *Desmodium*, *Dioclea*, *Dolichos*, *Dorycnium*, *Dunbaria*, *Eriosema*, *Eysenhardtia*, *Fagelia*, *Flemingia*, *Galactia*, *Grona*, *Hardenbergia*, *Hedysarum*, *Kennedya*, *Lonchocarpus*, *Mucuna*, *Onobrychis*, *Ornithopus*, *Periandra*, *Phaseolus*, *Platycamus*, *Pueraria*, *Robinia*, *Sesbania*, *Shuteria*, *Spatholobus*, *Teramnus*, *Tetragonolobus*, *Vigna*.
- (ii) Secretory cells in the cortex, phloem, and pith in species of *Dalbergia* (frequency varying considerably in different species), *Derris*, *Erythrina*, *Indigofera*, *Lespedeza*, *Mundulea*, *Pterocarpus*, *Rhynchosia* (very numerous), *Wistaria*.
- (iii) In the pith in *Adesmia*, *Aeschynomene*, *Anthyllis*, *Arachis*, *Cladrastis*, *Coronilla*, *Crotalaria*, *Desmodium*, *Diphaca*, *Hippocrepis*, *Leptodesmia*, *Lespedeza*, *Lonchocarpus*, *Lotus*, *Nissolia*, *Ornithopus*, *Ougeinia*, *Pseudarthria*, *Securigera*, *Zornia*.
- (iv) In the pith and primary cortex in *Adesmia*, *Apios tuberosa* Moench (numerous, small, arranged in a compact zone below the epidermis), *Calophaca*, *Chadsia*, *Dolichos*, *Erythrina*, *Hosackia*, *Scorpiurus*, *Stylosanthes*.
- (v) Accompanying the pericyclic fibres in *Amorpha*, *Chapmannia*, *Desmodium*, *Discolobium*, *Ebenus*, *Eversmannia*, *Eysenhardtia*, *Glycyrrhiza*, *Hedysarum*, *Indigofera*, *Leptodesmia*, *Lessertia*, *Lotus*, *Milletia*, *Mundulea*, *Olneya*, *Onobrychis*, *Ornithopus*, *Petalostemon*, *Psoralea*, *Robinia*, *Taverniera*, *Uraria*.
- (vi) In the primary cortex in *Alhagi*, *Alysicarpus*, *Anthyllis barba-jovis* Linn. (especially large, arranged in longitudinal series and forming a definite zone), *Apios*, *Astragalus*, *Clitoria*, *Cordyla*, *Coronilla*, *Dalea*, *Hedysarum*.
- (vii) In the sub-epidermis in *Alhagi*, *Taverniera*.
- (viii) In the epidermis in *Lathyrus pratense* Linn.
- (ix) In the primary phloem in *Alhagi*, *Eversmannia*, *Hammatolobium*, *Psoralea*, *Rhynchosia*.
- (x) In the cortex and phloem in species of *Castanospermum* and *Desmodium*.

- (xi) Distribution of tanniniferous cells in *Glycyrrhiza glabra* Linn. observed to be somewhat distinctive as follows. (a) As an almost continuous, compact layer of small cells in the epidermis and sub-epidermis. (b) As occasional scattered cells in the outer part of the cortex. (c) As longitudinal series of elongated cells in the phloem, solitary or in groups of 3-6. (d) As scattered longitudinal series in the pith.

(b) Similar secretory cells, but devoid of tanniniferous contents and therefore not stained brown, occur in a number of genera.

Secretory cavities (see also 'Leaf') of various types such as those illustrated in Fig. 106 also occur notably in the Galageae, e.g. in the phloem and pith of *Robinia viscosa* Vent.; similar cavities also observed in the phloem and pith of *Fagelia* sp., in the phloem of *Canavalia* sp., and in the cortex of *Derris malaccensis*. Solereder records the existence of secretory cavities situated in lumps on young branches of certain species of *Dalea*. Cells or lacunae containing mucilage also recorded in the secondary cortex and/or pith of species of *Alhagi* and *Halimodendron*.

Small **secretory canals** observed in the outer cortex and at the periphery of the pith in *Derris malaccensis*; larger ones also occur in the outer part of the cortex in *Myroxylon balsamum* var. *pereirae*. Secretory canals lined with epithelium recorded by Holm (993) in *Apios*.

Solitary **crystals** observed at Kew in the cortex in species of *Anthyllis*, *Apios*, *Caragana*, *Castanospermum*, *Chorizema*, *Cladrastis*, *Dalbergia*, *Derris*, *Desmodium*, *Erythrina*, *Galega*, *Glycine*, *Glycyrrhiza*, *Indigofera*, *Lathyrus*, *Lespedeza*, *Lonchocarpus*, *Medicago*, *Myroxylon*, *Ononis*, *Oxytropis*, *Platyosprion*, *Psoralea*, *Robinia*, *Sophora*, *Trifolium*, *Vicia*, *Wistaria*; in the phloem in species of *Anthyllis*, *Castanospermum*, *Cladrastis*, *Dalbergia*, *Desmodium*, *Erythrina*, *Glycyrrhiza*, *Halimodendron*, *Platyosprion*, *Robinia*, *Sophora*; in the pith in species of *Castanospermum*, *Indigofera*, *Myroxylon*, *Platyosprion*, *Robinia*, *Sophora*, *Wistaria*. Cluster crystals observed only in the cortex of *Erythrina crista-galli* Linn., and distinctive I-shaped crystals in the pith of *Robinia viscosa*. Crystals of the same types as those described above under 'Leaf' (p. 510) also occur in the stem.

STEMS WITH SPECIAL FEATURES

Certain species, especially but not exclusively amongst the xeromorphic members of the family, exhibit a considerable range of anatomical peculiarities, the precise nature of which cannot be fully described here. The following particulars concerning a selection of interesting species gives some indication of the unusual types of stem structure which have been observed by Dr. C. L. Hare in material grown at Kew.

(i) ASTRAGALUS AMBIGUUS BUNGE.

Xylem in young stems very loose in texture, divided into sectors by broad medullary rays. Vessels small, very thick-walled, solitary or in short tangential clusters, with reticulate thickening. Ground-mass of the wood composed mostly of thin-walled parenchyma, interspersed with small patches of fibres.

(ii) *CARAGANA ARBORESCENS* LAM. AND *C. MICROPHYLLA* LAM.

Young stems prominently ribbed, with strands of fibres in the angles between the ribs. Ribs and fibres later becoming exfoliated owing to the development of a broad band of cork in the cortex. Xylem very close in texture; vessels in uniseriate tangential bands embedded in parenchymatous ground tissue; rays very narrow.

(iii) *CARMICHAELIA AUSTRALIS* R. BR.

Young stem constituting a typical phylloclade. Stomata numerous, arranged transversely to the longitudinal axis of the stem. Cortex consisting of alternating radial bands of sclerenchyma and collenchyma. Stems becoming circular when older, through the exfoliation of the outer tissues following the development of deep-seated cork. Xylem in the form of wedge-shaped masses, separated by broad medullary rays. Vessels mostly in tangentially extended clusters; walls with delicate spiral (tertiary) thickening.

(iv) *CYTISUS*, *GENISTA*, *ULEX*, AND RELATED GENERA

The xeromorphic assimilatory stems of different species of *Cytisus* and related genera can often be distinguished by variations in the arrangement of the ribs, sclerenchyma, assimilatory tissue, as well as by differences in the occurrence and distribution of hairs. As an example of the type of structure in *Cytisus* the following particulars of *C. albus* Link. are given. Exterior of the stem with 18–20 prominent ribs, the distal ends of which are tangentially expanded as seen in transverse sections. Grooves between the ribs lined with hairs. Palisade chlorenchyma forming an almost continuous zone except where interrupted by wedge-shaped strands of thick-walled fibres within each of the ridges. *Cytisus scoparius* (L.) Link. similar, but provided with only 5 narrow ridges, hairs being absent from the grooves between them. *Genista cinerea* DC. similar to *Cytisus albus*, but with cortical vascular bundles in some of the ridges. Ribs less pronounced and grooves more shallow in *Genista hispanica* Linn. than in *G. cinerea*. Stomata of *G. hispanica* raised, with a characteristic pear-shaped vestibule almost closed by cuticular ridges. Chlorenchyma in the same species not arranged as a palisade. Young stems of *Ulex europaeus* Linn. with 8–10 ribs separated by narrow grooves. Stem clothed with twisted, uniseriate hairs. Each stomata with its long axis parallel to that of the stem. Cortical vascular bundles absent from the ridges.

The anatomy of the spines of *Ulex europaeus* has been described by Skipper (2119), from whose paper the following details are taken. Pith consisting of thick-walled cells, surrounded by a ring of vascular bundles. Cortex grooved, the grooves being equal in number to but alternating with the bundles. Ridges between the grooves supported by a strip of sclerenchyma, consisting of long, thick-walled fibres with simple pits. Ridges flanked by palisade-like chlorenchyma. Stomata mostly confined to the region of the palisade cells.

(v) *LATHYRUS* AND *VICIA*

Stem of *Lathyrus maritimus* Bigel flattened on one side and provided with 2 wings each containing a vascular bundle. Remaining vascular bundles widely spaced and arranged in a flattened circle around the hollow pith. Secretory tissue absent. Structure similar in *L. pratensis* Linn., but abundant

secretory cells present in the epidermis. Wings in *L. sylvestris* Linn. much longer than in the above 2 species, with several vascular bundles in each wing. The 2 wings of *Vicia cracca* Linn. each contain a single bundle.

According to Parsa (1657) the stem of *Lathyrus szowitsii* Boiss., a species endemic to Iran, is provided with exceptionally long wings with swollen distal ends. Each wing contains several small vascular bundles, whilst the swollen ends are supported by well-developed strands of sclerenchyma.

Apart from the preceding records and observations, the assimilatory stems of various members of the Papilionaceae have also been the object of several previous investigations, *Cytisus*, *Genista*, *Lebeckia*, and *Spartium* having been most thoroughly examined. Some of the earlier work has been summarized by Solereder, but more recent investigations include those by Pellegrin (1682), Jolivet (1187), and Taylor (2239). Less extensive observations have also been recorded by Goodlatte (795), Buchegger (303), Gravis (804), Evenari (Schwarz) (665). Pellegrin found the distribution of cortical bundles, the nature and arrangement of the ribs, and the nodal anatomy to be taxonomically important, but it was seldom possible to distinguish species by means of the stem structure alone. Jolivet likewise found the genera to be more or less clearly defined, but was unable to separate species with precision. Taylor, working mainly with *Cytisus* and *Genista*, found that the species could be roughly grouped by the appearance of the stem in transverse section. He divided them into five classes based on the number and shape of the ribs and variations in the distribution of fibres, cortical bundles, and assimilatory tissue. It is noteworthy that the earlier French work was apparently unknown to Taylor when his researches were in progress.

Lacoste (1312) has described the phyllode of *Phylloxylon* as having numerous stomata in the epidermis, palisade chlorenchyma beneath both surfaces, while the vascular bundles are widely spaced and arranged in a flattened ring. The centre is occupied by a pith-like tissue.

The stems of 'weeping' varieties of *Sophora japonica* Linn. and *Caragana arborescens* Lam. were found by Löw (1397) to have fewer phloem fibres and less fully developed prosenchymatous elements in the xylem than the erect forms of the same species. The difference was first apparent during the second year's growth.

× *Laburnocytisus adamii* Schneid. (syn. *Laburnum adamii* Schneid.) is generally regarded as a periclinal chimaera in which the skin of tissue derived from *Cytisus purpurea* Vent. covers more deeply seated tissue derived from *Laburnum anagyroides* Med. (syn. *L. vulgare* Bercht. et Prsl.). Anatomical evidence, which he believed to support this interpretation, was obtained by Buder (305). Since the epidermal cells of *Cytisus purpurea* are richer in tannin than those of *Laburnum anagyroides* the presence of tannin could be used for the detection of 'purpurea' cells in the graft hybrid. When sections of the leaves or petiole were placed in a solution of potassium bichromate the dark-brown 'purpurea' epidermis was clearly visible to the naked eye, and contrasted strongly with the uncoloured 'vulgare' tissues beneath. In older stems the mode of cork formation also helped to distinguish the tissues of the two parents. In *C. purpurea* cork arises in the epidermis, in *L. anagyroides* its origin is more deep-seated. In *L. adamii* cork originates in both positions, but cork formation does not persist for so long in the 'purpurea' epidermis as in the more deep-

seated 'vulgare' tissues, so that eventually the outer 'purpurea' tissues are cast off and an old stem is thus derived wholly from *L. anagyroides*. Buder's thorough anatomical investigation failed to reveal any facts which are contrary to the concept that *L. adamii* is a periclinal chimaera.

According to Holm (993) the tuber at the base of the stem of *Apios tuberosa* Moench. includes numerous small vascular strands in the pith, each containing secretory canals of the same type as those in other parts of the plant.

WOOD (Figs. 115, 116, and 117)

Vessels medium-sized (100–200 μ mean tangential diameter) in most genera; very small (less than 50 μ) in *Anagyris*, *Anthyllis*, *Apoplanesia*, *Ateleia*, *Behaimia*, *Belairia*, *Benthamantha*, *Brya*, *Calycotome*, *Cytisus*, *Drepanocarpus*, *Halimodendron*, *Lespedeza*, *Medicago*, and *Poecilanthus*; moderately small (50–100 μ) in *Aeschynomene*, *Desmodium*, *Indigofera*, *Lupinus*, *Piptanthus*, *Piscidia*, *Podalyria*, *Sabinea*, *Schefflerodendron*, *Spartium*, *Swartzia* p.p., and *Zollernia*; large (more than 200 μ) in some species of *Andira*, *Bowdichia*, *Cassipouia*, *Castanospermum*, *Clathrotropis*, *Dalbergia*, *Dussia*, *Erythrina*, *Hymenolobium*, *Kunstleria*, *Milletia*, *Monopteryx*, *Ostryocarpus*, *Platycyamus*, *Platymiscium*, and *Pongamia*; very large in some of the lianes, e.g. reaching a diameter of 600 μ in species of *Entada*, according to Solereder; occasionally of 2 distinct sizes, e.g. in *Butea superba* Roxb. the larger vessels are up to 425 μ in diameter and the smaller not more than 175 μ ; in other species, particularly those with an oblique or tangential pattern, the larger vessels may themselves be small and be set in a matrix of extremely small, angular storied vessels that are comparable with tracheids in cross-section, e.g. in *Dioclea*, *Halimodendron*, *Spartium* (Fig. 116 D), *Ulex*, and *Wistaria*; the tendency for the vessels to be mostly solitary, but with a few multiples and clusters, noted as characteristic of many of the genera of the Mimosaceae and Caesalpiniaceae, is not particularly noticeable in the Papilionaceae; in woods without any definite radial pattern radial multiples are usually moderately abundant, but do not commonly exceed 3 cells except in some species of *Belairia*, *Dalbergia*, *Medicago*, and *Pterocarpus*; irregular clusters are common in some species of *Coursetia*, *Crotalaria*, *Dalbergia*, *Dalea*, *Daviesia*, *Platymiscium*, *Pterocarpus*, *Pueraria*, *Retama* (1493), and *Sophora*; with an oblique pattern in some species of *Anthyllis*, *Calycotome*, *Cytisus*, *Dalea*, *Genista*, *Laburnum*, *Parosela*, *Pickeringia*, *Sophora*, *Spartium* (Fig. 116 D), and *Ulex*, and with a tangential pattern in *Anagyris*, *Halimodendron*, *Lupinus*, *Piptanthus*, *Podalyria*, *Robinia*, and *Virgilia*; clusters common in nearly all these woods with a distinct vessel pattern; apart from the woods with very numerous vessels in oblique or tangential rows, most species have either fewer than 5 vessels per sq. mm. or between 20 and 40 per sq. mm.; fewer than 5 per mm. in species with large vessels and also in *Aeschynomene*, *Afrormosia*, *Alexa*, *Amerimnon*, *Andira*, *Baphia*, *Butea*, *Canavalia*, *Cassipouia*, *Coumarouna*, *Crotalaria*, *Derris*, *Dipteryx*, *Fordia*, *Inocarpus*, *Machaerium*, *Milletia*, *Muelleria*, *Ormosia*, *Ougeimia*, *Piscidia*, *Poecilanthus*, *Pongamia*, *Pterodon*, *Tipuana*, *Torresia*, and *Zollernia*; 5–20 per sq. mm. in *Desmodium* (Janssonius 1154), *Haplormosia*, *Pericopsis*, *Pueraria*, *Rothia*, *Schefflerodendron*, *Sophora* p.p., *Spatholobus*, *Swartzia*, *Sweetia*, and *Wistaria*; more than 40 per mm. in *Brya*, *Eysenhardtia*, and *Medicago*; ring-porous or semi-ring-porous

in at least some species of *Ammodendron*, *Amorpha*, *Anthyllis*, *Calycotome*, *Cascaronia* (1864), *Cladrastis*, *Cytisus*, *Dalbergia*, *Dalea*, *Edwardsia* (1886), *Eysenhardtia*, *Genista*, *Gourliea*, *Halimodendron*, *Indigofera* (1851), *Laburnum*, *Lespedeza*, *Parosela*, *Pickeringia*, *Podalyria*, *Pterocarpus*, *Robinia*, *Sophora*,

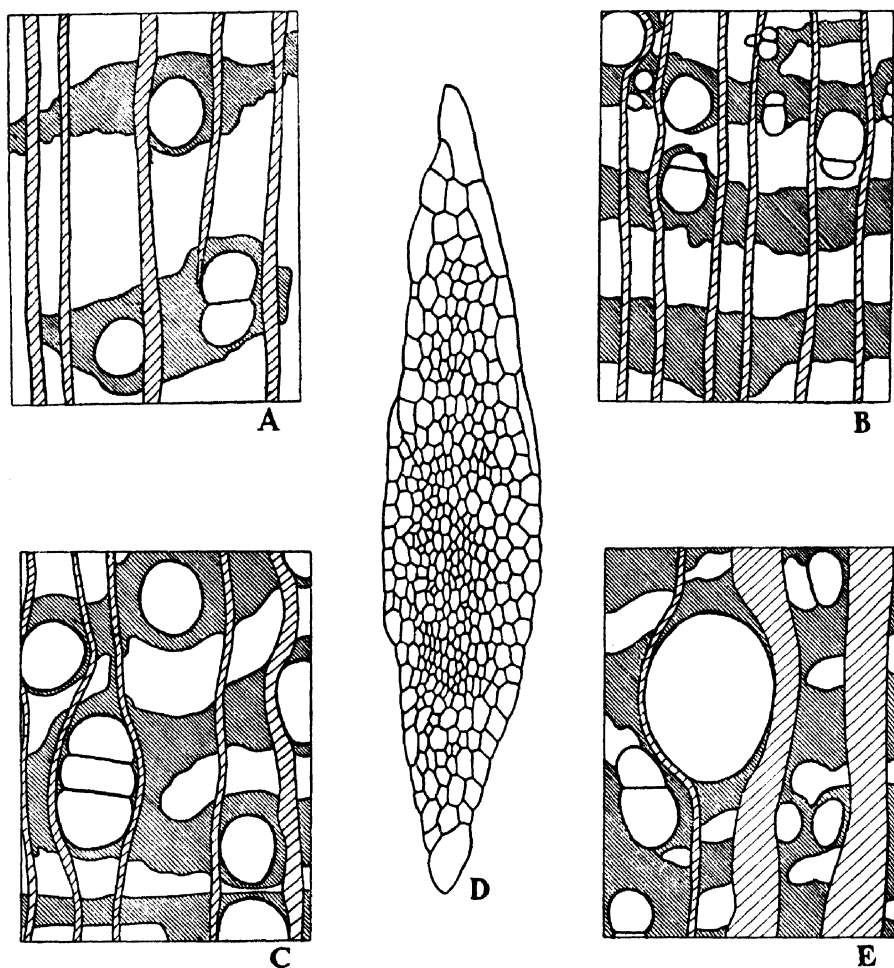


FIG. 115. LEGUMINOSAE—PAPILIONACEAE

A, *Pericopsis mooniana* Thw. B, *Millettia pendula* Benth. C, *Afrormosia laxiflora* Harms. D, *Erythrina stricta* Roxb. E, *Butea superba* Roxb.

Spartium, *Ulex*, *Virgilia*, and *Wistaria* (1851); spiral thickening, often limited to the smaller vessels, observed or reported in *Amphithalea* (1851), *Anagyris*, *Argyrolobium* (1851), *Calycotome*, *Coelidium* (1851), *Cytisus*, *Erinacea* (1851), *Genista*, *Halimodendron*, *Laburnum*, *Lathlogyna* (1851), *Lebeckia* (1851), *Liparia* (1851), *Lotononis* (1851), *Petteria* (1851), *Pickeringia*, *Platylobium* (1851), *Podalyria*, *Priestleya* (1851), *Robinia*, *Sophora*, *Spartium*, *Ulex*, and *Wistaria*; Solereder refers also to spirally thickened 'tracheids or vessels of

narrow lumen' in species of *Adenocarpus*, *Ammodendron*, *Anthyllis*, *Caragana*, *Carmichaelia*, *Cladrastis*, *Colutea*, *Coronilla*, *Cyclopia*, *Dorycnium*, *Edwardsia*, *Lotus*, and *Sweetia*. Perforations simple. Intervascular pitting alternate, typically small; minute in *Brya*, *Dipteryx*, *Lepedeza*, *Myrocarpus*, *Piscidia*, *Schefflerodendron*, *Toluijera*, and *Zollernia*; pits moderately large in a few species, e.g. *Butea superba* Roxb., *Centrolobium paraense* Tul., *Drepanocarpus inundatus* Mart., *Pericopsis mooniana* Thw., and *Spatholobus roxburghii* Benth. and large in *Hymenolobium* and *Kunstleria*; occasionally with conspicuous striations due to coalescent apertures, e.g. in *Rothia* sp. and *Dalea spinosa* Gray; pits to parenchyma and ray cells usually similar to the intervacular pits, but sometimes either simple or subtending larger parenchyma pits in *Gliricidia*, *Hebestigma*, *Hymenolobium*, *Kunstleria*, *Pericopsis*, *Piscidia*, *Platymiscium* p.p., *Robinia*, *Sabinia*, and *Spatholobus*, and, according to Solereder, in *Brya*; sometimes elongated in *Dioclea*; pits vested. Solid deposits common, tyloses abundant in some species of *Amorpha*, *Coursetia*, *Dalbergia*, *Gliricidia* (1886), *Hebestigma*, *Lennea*, *Machaerium*, *Notodon* (1886), *Olneya* (1886), *Robinia*, and *Sabinea*; those of *Sabinea florida* DC. containing crystals. Mean member length 0.1–0.4 mm. **Parenchyma** usually moderately to very abundant and either predominantly paratracheal or in moderately regular bands that tend to be replaced by definitely paratracheal forms where the parenchyma is less abundant; round or diamond-shaped sheaths, such as are characteristic of the Mimosaceae and Caesalpinjiaceae, occur in some genera but are less common than the confluent or other banded types. Very abundant, in broad, moderately regular bands 4 or more cells wide in some species of *Bergeronia*, *Butea*, *Clitoria*, *Desmodium* p.p. (1154), *Erythrina*, *Fordia*, *Inocarpus*, *Lonchocarpus*, *Milletia* (Fig. 115 B), *Muelleria*, *Piscidia*, *Pongamia*, and *Spatholobus*; in narrower bands in *Alexa* p.p., *Baphia* (Fig. 116 J), *Brya*, *Dalbergia* p.p., *Drepanocarpus*, *Geoffroea*, *Haplormosia*, *Machaerium*, *Platypodium*, *Pterocarpus* p.p., *Schefflerodendron*, *Swartzia* p.p., and *Zollernia*; confluent, forming irregular bands or the matrix for oblique or tangential bands of vessels, in species of *Afrormosia* (Fig. 115 C), *Alexa* p.p., *Anagyris*, *Andira*, *Anthyllis*, *Belairia*, *Bergeronia*, *Calycotome*, *Canavalia*, *Cashalia*, *Clathrotropis*, *Coursetia*, *Cytisus*, *Dalbergia*, *Dalea*, *Derris*, *Dussia*, *Ecastophyllum*, *Erythrina*, *Etaballia*, *Genista*, *Gliricidia*, *Gourliea*, *Halimodendron*, *Hebestigma*, *Hymenolobium*, *Ichthyomethia*, *Laburnum*, *Lonchocarpus*, *Lupinus*, *Ostryocarpus*, *Parosela*, *Pickeringia*, *Piptanthus*, *Piscidia*, *Platycyamus*, *Podalyria*, *Poecilanthe*, *Pongamia*, *Pterocarpus*, *Retama* (1493), *Sabinea*, *Spartium*, *Swartzia* p.p., and *Ulex*; intermediate between aliform and confluent in *Dalbergia* p.p., *Desmodium* p.p., *Diphysa*, *Indigofera*, *Inocarpus* (1154), *Medicago*, *Paramachaerium*, *Pericopsis*, *Platymiscium*, *Pterocarpus* p.p., and *Tipuana*; aliform, sometimes confluent at the end of the growth ring, in *Amherstia*, *Ateleia*, *Bowdichia*, *Castanospermum*, *Coumarouna*, *Diploptropis*, *Harpalyce*, *Kunstleria*, *Lepedeza*, *Monopteryx*, *Myrospermum*, *Ormosia*, *Ougeinia*, *Sophora* p.p., and *Torresia*; in predominantly rounded sheaths about the vessels (vasicentric) in *Amorpha*, *Apoplanesia*, *Behaimia*, *Brya*, *Cladrastis* (confluent in outer part of ring), *Crotalaria*, *Dalea*, *Dioclea*, *Eysenhardtia*, *Indigofera*, *Myrocarpus*, *Myroxylon*, *Rhynchosia*, *Robinia* (confluent in outer part of ring), *Rothia*, *Sesbania*, *Sophora*, *Toluijera*, and *Virgilia*; in a narrow layer on the abaxial sides of the vessels in *Centrolobium* and

Sweetia; scattered strands (diffuse), which are sometimes crystalliferous, present in *Amerimnon*, *Andira*, *Bowdichia*, *Brya* (very conspicuous),

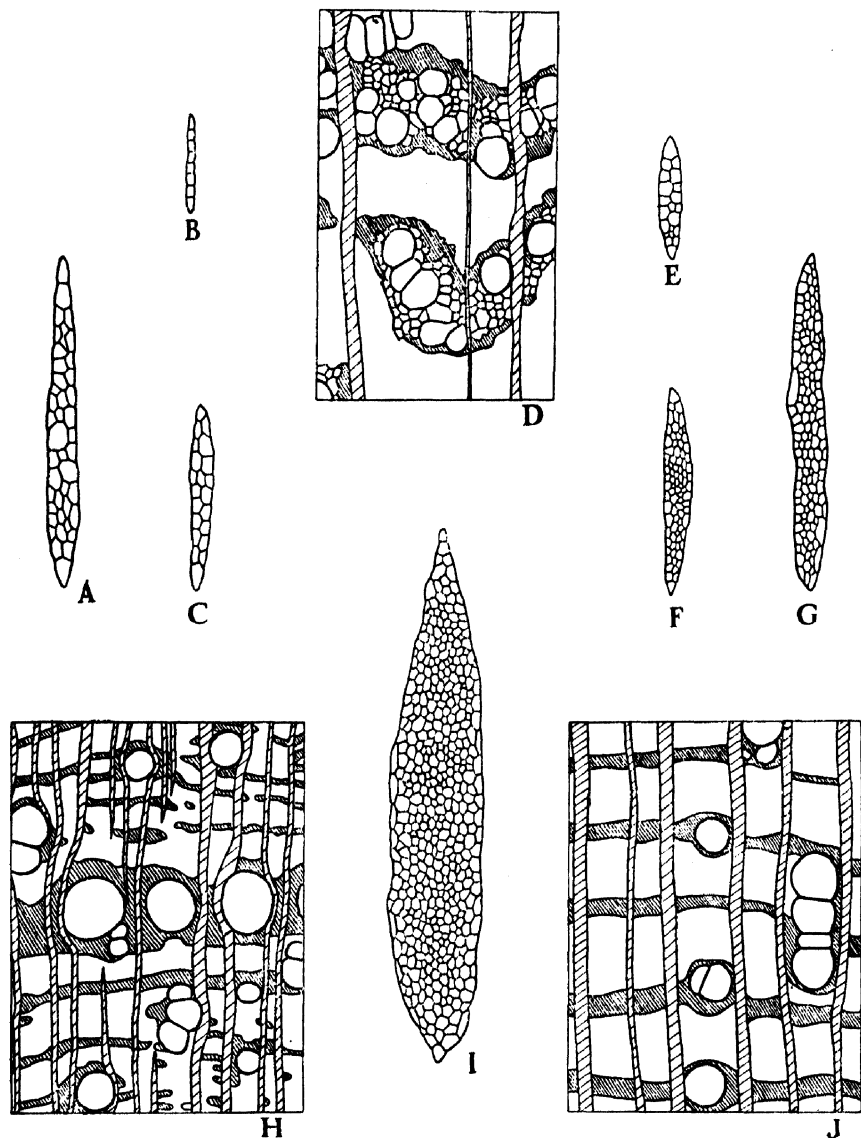


FIG. 116. LEGUMINOSAE—PAPILIONACEAE

A, *Andira inermis* H. B. et K. B, *Pterocarpus stevensonii* Burtt Davy. C, *Millettia atropurpurea* Benth. D, *Spartium junceum* Linn. E, *Dalbergia nigra* Allem. F, *Cladrastis amurensis* Benth. G, *Sarothamnus scoparius* (L.) Koch. H, *Dalbergia melanoxydon* Guill. I, *Laburnum anagyroides* Med. J, *Baphia nitida* Lodd.

Centrolobium, *Cladrastis*, *Dalbergia* (a few species only), *Diphysa*, *Genista*, *Machaerium*, *Myrocarpus*, *Pterocarpus* (a few species), *Toluifera*, and *Ulex*; in

Pueraria there are both vasicentric sheaths (paratracheal) and short, apparently apotracheal bands; in *Wistaria* the parenchyma mixed with very small vessels tends to form the ground tissue and in *Aeschynomene* parenchyma constitutes the greater part of the tissues and forms a ground-mass in which groups of fibres and vessels appear on cross-section as aliform patches (Fig. 117 A); terminal parenchyma present in some genera. Chambered crystals present in the marginal cells of the paratracheal or banded parenchyma of most of the species but not observed in *Alexa*, *Ammodendron*, *Amorpha*, *Anagyris*, *Apoplanesia*, *Bowdichia*, *Calycotome*, *Canavalia*, *Cladrastis*, *Crotalaria*, *Cytisus*, *Dalea*, *Daviesia*, *Diphysa*, *Dussia*, *Eysenhardtia*, *Genista*, *Halimodendron*, *Hebestigma*, *Kunstleria*, *Laburnum*, *Lespedeza*, *Lupinus*, *Medicago*, *Monopteryx*, *Paramachaerium*, *Parosela*, *Pericopsis*, *Pickeringia*, *Piptanthus*, *Podalyria*, *Poecilanthus*, *Pueraria*, *Rothia*, *Sabinea*, *Schefflerodendron*, *Sesbania*, *Sophora*, *Spartium*, *Torresia*, *Ulex*, *Virgilia*, and *Vouacapoua*; chambered crystals sometimes occurring also in diffuse parenchyma, where this is present (see p. 524); the maximum number of crystals per strand typically about 8 and not more than 11, but 12 or more in some genera, particularly those in which the ordinary strands are commonly of 4 cells and also in some woods with strands of not more than 2 cells, e.g. *Bergeronia*, *Brya*, *Muelleria*, and *Zollernia*. In *Aeschynomene elaphroxylon* Guill. et Perr. the crystals are usually limited to a layer of cells adjoining the adaxial side of the fibre groups and the chambered strands are sometimes locally biseriate. Cells sometimes containing gum-like deposits. Record and Hess (1886) note small patches of sclerotic cells in *Clathrotropis*. Strands most commonly of 1-2, or only 1 cell, but of 2-4 cells in a number of genera, e.g. *Afrormosia*, *Alexa*, *Andira*, *Bowdichia*, *Centrolobium*, *Diplotropis*, *Dipteryx*, *Haplormosia*, *Hymenolobium*, *Lonchocarpus*, *Lupinus*, *Milletia*, *Myrocarpus*, *Myroxylon*, *Ormosia*, *Pericopsis*, *Piscidia*, *Platymiscium* p.p., *Pterocarpus* p.p., *Robinia*, *Rothia*, *Schefflerodendron*, *Sesbania*, *Spatholobus*, *Swartzia*, *Sweetia*, *Torresia*, *Virgilia*, and *Wistaria*; strands of more than 4 cells present in occasional genera, e.g. *Kunstleria*, *Monopteryx*, and *Pueraria*; fusiform parenchyma cells common in *Anagyris*, *Baphia*, *Butea* p.p., *Cladrastis*, *Dalbergia*, *Desmodium* (1154), *Diphysa*, *Erythrina*, *Geoffraea*, *Gourliea*, *Laburnum*, *Paramachaerium*, *Parosela*, *Platymiscium* p.p., *Podalyria*, *Pterocarpus* p.p., *Sophora*, and *Torresia*, and with the parenchyma cells almost exclusively fusiform in *Aeschynomene*, *Calycotome*, *Cytisus*, *Genista*, *Indigofera*, *Spartium*, and *Ulex*. Strands typically distinctly storied, but the stories rather vague in or absent from *Alexa*, *Amherstia*, *Amorpha*, *Anthyllis*, *Apoplanesia*, *Bowdichia*, *Butea* p.p., *Cassia*, *Centrolobium* p.p., *Crotalaria*, *Diplotropis*, *Harpalyce*, *Hebestigma*, *Hymenolobium*, *Lespedeza*, *Monopteryx*, *Ormosia*, *Pericopsis*, *Piscidia*, *Platymiscium* p.p., *Pongamia*, *Pterygopodium*, *Pueraria*, *Rothia*, *Sabinea*, *Schefflerodendron*, *Sesbania*, *Spatholobus*, *Swartzia*, *Torresia*, *Vouacapoua*, *Virgilia*, *Wistaria*, and *Zollernia*. Many of the woods with strands predominantly of 2 cells exhibit secondary storying of the parenchyma owing to the regular position of the central cross-wall. Distinctly storied strands have obtuse-angled gable-ends on tangential section and the pitting is sometimes markedly more abundant on these end walls, e.g. in *Aeschynomene elaphroxylon*. This species was investigated in great detail by Beijer (168) in his work on cell division in the cambium leading to storied structure. Janssonius (1154)

uses the presence of these two characters as a means of distinguishing the Papilionaceae from the Mimosaceae and Caesalpinaceae, but there appear to be many exceptions. According to Solereder, the wood parenchyma in some of the lianes is thin-walled and unligified, especially in the later-formed secondary wood, e.g. in species of *Dioclea*, *Mucuna*, *Phaseolus*, and *Pueraria*; axial wood of denser structure occurs in the neighbourhood of the pith. **Rays** of more than half the genera 2–3 cells wide; exclusively uniseriate or with only occasional biseriate rays in some species of *Canavalia*, *Centrolobium*, *Coumarouna*, *Dipteryx*, *Drepanocarpus*, *Etaballia*, *Geoffraea*, *Gourliea*, *Inocarpus*, *Kunstleria*, *Machaerium*, *Myroxylon* (2430), *Paramachaerium*, *Piscidia*, *Platymiscium*, *Platypodium*, *Pterocarpus*, *Spartium*, *Swartzia* p.p., and *Tipuana*; 4–10 cells wide in *Afrormosia*, *Ammodendron*, *Anagyris*, *Andira*, *Anthyllis*, *Baphia*, *Benthamantha*, *Butea*, *Cladrastis*, *Clitoria*, *Cytisus*, *Dalea*, *Desmodium*, *Dioclea*, *Erythrina*, *Halimodendron*, *Ichthyomethia*, *Indigofera*, *Laburnum*, *Lonchocarpus*, *Lupinus*, *Medicago*, *Milletia*, *Monopteryx*, *Parosela*, *Piptanthus*, *Platycyamus*, *Retama* (1493), *Robinia*, *Sophora*, *Spartium*, *Spatholobus*, and *Ulex*; sometimes more than 10 cells wide in the larger rays of *Erythrina*, *Laburnum*, and in the interfascicular rays of *Pueraria* and *Wistaria*; with some very large rays, 20–30 cells wide in *Aeschynomene* and *Monopteryx* and, according to Solereder, in some species of *Sarothamnus*; of 2 distinct sizes, the small rays storied, in *Aeschynomene*, *Daviesia*, and *Milletia albiflora* Prain, and, without storying of the small rays, in *Monopteryx*; up to more than 1 mm. in height in *Aeschynomene*, *Andira*, *Baphia*, *Clathrotropis*, *Clitoria*, *Coursetia*, *Erythrina*, *Fordia*, *Hebestigma*, *Laburnum*, *Lennea*, *Lupinus*, *Medicago*, *Milletia* p.p., *Monopteryx*, *Ostryocarpus*, *Parosela*, *Pickeringia*, *Piptanthus* (small stem), *Pueraria* (interfascicular), *Sophora*, *Spatholobus*, and *Wistaria* (interfascicular); woods with multiseriate rays usually with few uniseriates, e.g. *Afrormosia*, *Andira*, *Baphia*, *Bergeronia*, *Butea*, *Cladrastis*, *Dalbergia* p.p., *Drepanocarpus*, *Erythrina* p.p., *Halimodendron*, *Haplormosia*, *Hymenolobium*, *Laburnum*, *Lonchocarpus*, *Medicago*, *Monopteryx*, *Muelleria*, *Myrocarpus*, *Myroxylon*, *Ougeneia*, *Pericopsis*, *Platycyamus*, *Podalyria*, *Pongamia* p.p., *Robinia*, *Schefflerodendron*, *Sophora* p.p., *Spartium*, *Spatholobus*, *Torresia*, and *Vouacapoua*; mostly from 4 to 12 rays per mm.; more than 12 per mm. in some species of *Amorpha*, *Belairia*, *Bergeronia*, *Brya*, *Calycotome*, *Dalbergia*, *Dalea*, *Dipteryx*, *Drepanocarpus*, *Ecastophyllum*, *Etaballia*, *Geoffraea*, *Gourliea*, *Hebestigma*, *Inocarpus*, *Machaerium*, *Parosela*, *Platypodium*, *Podalyria*, *Pterocarpus*, *Sabinea*, and *Swartzia*; with fewer than 4 rays per mm. in *Bowdichia*, *Erythrina*, *Halimodendron*, and *Pueraria*; homogeneous (Kribs's Types I, II, and III) in *Alexa*, *Anagyris*, *Andira*, *Anthyllis*, *Baphia*, *Benthamantha*, *Bergeronia*, *Brya*, *Butea*, *Cashalia*, *Centrolobium*, *Clathrotropis*, *Coumarouna*, *Daviesia*, *Derris*, *Desmodium*, *Dipteryx*, *Dussia*, *Erythrina* p.p., *Etaballia*, *Fordia*, *Geoffraea*, *Gliricidia*, *Halimodendron*, *Haplormosia*, *Ichthyomethia*, *Inocarpus*, *Lennea*, *Lonchocarpus*, *Machaerium*, *Milletia*, *Muelleria*, *Ostryocarpus*, *Paramachaerium*, *Pericopsis*, *Piscidia*, *Platycyamus*, *Platymiscium*, *Platypodium*, *Pongamia*, *Pterocarpus*, *Robinia*, *Rothia*, *Schefflerodendron*, *Sophora*, *Spartium*, *Swartzia*, and *Ulex*; moderately heterogeneous (Kribs's Type II and occasionally III) with 1–2 marginal rows of square or upright cells in most of the other genera, but with 4 or more such rows in *Hebestigma*, *Indigofera*, *Kunstleria*, and *Lupinus*;

cells tending to be all square (radial section) in *Medicago* and *Parosela*; procumbent cells small in tangential diameter (less than $10\ \mu$) in some genera, e.g. *Anthyllis*, *Cladrastis*, *Cytisus*, *Desmodium*, *Diploptropis* p.p., *Genista*, *Halimodendron*, *Indigofera*, *Laburnum*, *Machaerium*, *Myrocarpus*, *Myroxylon*, *Pericopsis*, *Piscidia*, *Pongamia*, *Robinia*, *Schefflerodendron*, and *Sweetia*; sheath cells present in some species of *Butea*, *Clitoria*, *Cytisus*, *Dioclea*, *Erythrina*, *Halimodendron*, *Laburnum*, *Lupinus*, and *Spartium*; commonly containing gum-like deposits; crystals observed in only a few species, sometimes abundant, e.g. in *Parosela* and *Zollernia*. Usually storied in woods with low rays, but in most of the genera the rays are several times as high as the parenchyma strands and exhibit no storying; distinctly storied in some species of *Aeschynomene*, *Amorpha*, *Cascaronia* (576), *Castanospermum*, *Centrolobium*, *Cladrastis*, *Dalbergia*, *Dalea*, *Drepanocarpus*, *Laburnum*, *Machaerium*, *Paramachaerium*, *Pericopsis*, *Pickeringia*, *Pterocarpus*, *Robinia*, *Schefflerodendron*, *Sophora*, *Swartzia*, *Sweetia*, and *Zollernia*.

The rays of a few genera exhibit some unusual features. Solereder refers to the occurrence of spirally thickened tracheids in the secondary rays of *Cytisus ardoini* Fourn. and *C. sauzeanus* Burn. et Briqu.; the large rays of *Monopteryx uacu* Spruce include horizontal strands of thick-walled fibres; in *Aeschynomene elaphroxylon* most of the rays are uniseriate and storied, but in old material there are also broader rays containing vascular strands, which sometimes include 30 or more vessels, arranged, as seen in tangential section, in multiples and clusters of 2–6 cells; these vessels have simple perforations and numerous, rather large intervascular pits, which in some cases are elongated to an almost scalariform type; Solereder refers to smaller, spirally thickened vessels in the centre; he quotes Klebahn as having shown that the vascular strands correspond to the vascular part of the rudiments of roots formed between the broad rays and lenticels on the surface of the stem.

Fibres typically with few, small, simple pits, more numerous on the radial than on the tangential walls; pits numerous in a few species and occasionally moderately large, e.g. in *Alexa* and *Swartzia*; with conspicuous bordered pits in *Kunstleria*. Very occasionally septate in *Ougeneia*, *Robinia*, *Sophora*, and *Tipuana*. In the majority of genera walls moderately to very thick, but occasionally very thin-walled, e.g. *Lespedeza*, *Rothia*, and *Virgilia*; often with a gelatinous inner layer. In a few woods the fibres form small islands on the cross-section owing to the abundance of wood and ray parenchyma, e.g. in *Aeschynomene* (Fig. 117 A), *Butea* (Fig. 115 E), *Clitoria*, *Pueraria*, *Spatholobus*, and *Wistaria*; in *Aeschynomene elaphroxylon* the fibres form aliform patches about the vessels, similar in shape and distribution to aliform parenchyma. Mean length 0.6–1.7 mm. **Intercellular canals** of the vertical traumatic type observed or reported (1886) scattered throughout the ring in *Andira* and *Humboldtiella*. **Included (interxylary) phloem**, see under 'Anomalous Structure' below.

ANOMALOUS STRUCTURE

Anomalous structure, consisting of successive layers of xylem and phloem repeating the primary structure of the stem, separated by tangential bands of conjunctive parenchyma, observed in *Machaerium*, *Pueraria*, and *Wistaria* and reported by Solereder in *Derris*, *Mucuna*, *Pachyrhizus*, *Rhynchosia*,

Spatholobus, and *Strongylodon*; of the 'disperse' type, the stem cleft into irregular strands by dilation of the parenchymatous elements, in *Kunstleria ridleyi* Prain. The formation of successive rings of xylem and phloem in the primary cortex, pericycle, or, more rarely, in the phloem also recorded in

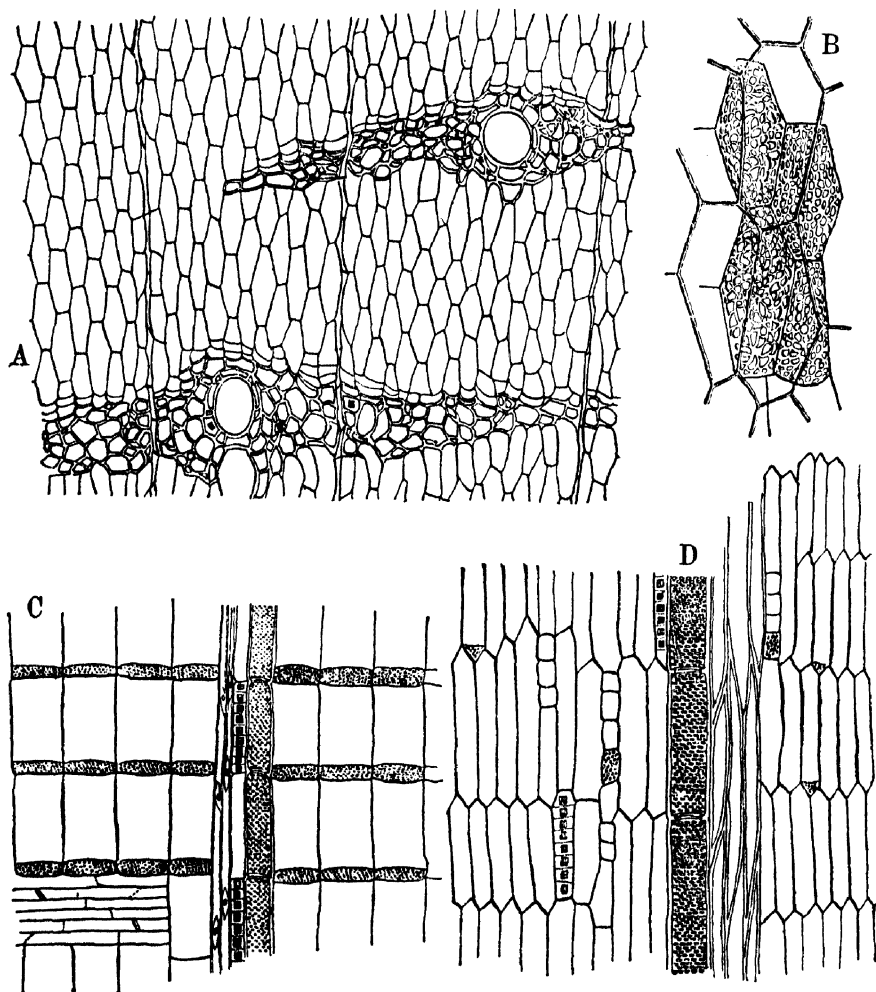


FIG. 117. LEGUMINOSAE—PAPILIONACEAE

Wood of *Aeschynomene* sp. A, Transverse section through the wood. B, Part of a transverse section showing the terminal surfaces of the transversely cut fibrous cells, which have wide lumina. C, Radial longitudinal section. D, Tangential section.—By Solereder.

species of *Pueraria* and *Wistaria* by Handa (882 A). Interxylary phloem recorded in species of *Dioclea*, *Mucuna*, *Phaseolus*, and, according to Russell (1793), in *Millettia*. Stems of lianes mostly cylindrical, but band-shaped in *Machaerium* and *Rhynchosia phaseoloides* DC. A method whereby the xylem becomes split up by the development from the cambium of a contractile tissue has been described by Ziegenspeck (2506).

ROOT

The roots of the Papilionaceae are interesting mainly on account of the almost universal occurrence on them of nodules or tubercles containing bacteria capable of fixing atmospheric nitrogen. For this reason leguminous crops are commonly grown as a green manure. A considerable volume of literature concerning this interesting subject exists, but is outside the scope of this book. In woody species such as *Wistaria sinensis* Sweet. the nodules, according to Jimbo (1181), consist of a chain of 1-4 swellings. Small lamellae termed 'palettes' have been described by Severini (2080) on the roots of *Hedysarum coronarium* Linn. One surface of these bodies becomes covered with absorbing hairs, whilst the other is flat, or at most provided with a few small papillae. The 'palettes' arise in the pericycle, and their number is controlled by the nature of the soil. They are quite distinct from root-nodules, and become calcified by the deposition of calcium carbonate within the living cells. According to Fehér (681) tannin occurs in smaller quantities in the young root of *Robinia pseudacacia* Linn. than in the aerial part of the plant, but short tanniniferous tubes are present beneath the bark. An oily substance occurs in young and old roots as well as in the tubercles of the same species, and tyloses develop in the xylem vessels in the third year. For further information concerning roots of the Papilionaceae see: Bond (226), Dastur and Saxton (542), Holm (993), Lindemuth (1373), Smith and Kersten (2149), Staber (2178), Ward (2360).

TAXONOMIC AND PHYLOGENETIC NOTES
(FOR THE LEGUMINOSAE IN GENERAL)

(i) FROM GENERAL ANATOMY

Dormer's (600, 601, 602) recent investigations, which refer mainly to the Leguminosae, lead him to conclude that phyllotaxy and the course of the primary vascular system provide characters of taxonomic and phylogenetic interest. He expresses the view that the 'evolution of a typical herbaceous habit becomes possible only when the tangential continuity of the vascular system is maintained by nodal anastomoses between the bundles, so that there is no necessity for the formation of a continuous cylinder of secondary tissues'. These interesting views will need to be substantiated by further investigations on a much wider range of material before their significance can be fully assessed. This will undoubtedly take time, because the technique involved does not permit large quantities of material to be examined very rapidly. Still more recently Dormer (605) has extended his line of inquiry by examining the phylogenetic significance of the pulvinus in the Papilionatae, the pulvinate tribes and genera being regarded as more primitive than those which are epulvinate.

(ii) FROM WOOD STRUCTURE

The wood anatomy in general suggests that the Mimosaceae are the least highly specialized and the Papilionaceae the most highly specialized of the three Leguminous families. For example, the following characters in the Papilionaceae indicate a higher degree of specialization than in the Caesalpiniaceae or the Mimosaceae: (a) very short cambial initials, with a consequent

higher proportion of woods with storied parenchyma and numerous fusiform cells, (b) vessel characters, e.g. the more common occurrence of ring-porousness, pronounced patterns, and spiral thickening, and (c) the more common occurrence of anomalous structure. The Mimosaceae, on the other hand, appears at first sight to have the most highly specialized rays of the three groups, in that the rays are always homogeneous and are typically composed of small cells and in that uniseriatae are typically few. The position may, perhaps, be better expressed, however, by saying that, though the Mimosaceae have achieved a more uniformly high level of ray development, the Caesalpiniaceae, and more especially the Papilionaceae, include both more highly specialized rays as well as less highly specialized types. The proportion of genera with septate fibres shows a suggestive decrease from the Mimosaceae to the Papilionaceae, with the Caesalpiniaceae intermediate, but the significance of this feature is not clear.

Finally it may be noted that there is less difference in general structure and in degree of specialization between the Mimosaceae and the Caesalpiniaceae than between the latter and the Papilionaceae. The principal features that tend to distinguish the three families are given below.

Normand (1915) states that in its wood anatomy *Ibadja walkeri* A. Chev. closely resembles *Loesenera kalantha* Harms and differs from both *Berlinia* and *Hymenostegia*.

Hess (1960) considers the wood anatomy supports the view that *Daubentonia texana* Pierce and *D. punicea* (Cav.) DC. may be separate genera and that *Senegalia angustifolia* (Lam.) Britt. et Rose should be separated from *Senegalia* and made into a monotypic genus.

Points of Difference between Mimosaceae, Caesalpiniaceae, and Papilionaceae

Vessels. Oblique or tangential pattern never more than vague in Mimosaceae, occasionally distinct in the Caesalpiniaceae, and very distinct in several Papilionaceae. Spiral thickening absent from Mimosaceae, more common in Papilionaceae than in Caesalpiniaceae. More commonly ring-porous in Papilionaceae. Gummy deposits common in all three groups but most pronounced in the Caesalpiniaceae.

Parenchyma. Round or diamond-shaped paratracheal typical of the Mimosaceae and Caesalpiniaceae and occurring in some Papilionaceae; diffuse, usually crystalliferous strands very common in Mimosaceae, common in Caesalpiniaceae, relatively rare in the Papilionaceae; terminal most pronounced in the Caesalpiniaceae, present in the others. Strands most commonly of 2 or 4 cells in Mimosaceae and Caesalpiniaceae, of 1–2 cells in the Papilionaceae. Fusiform cells common in a few genera of Mimosaceae and Caesalpiniaceae, common and sometimes predominant in several genera of Papilionaceae. Crystalliferous strands of more than 11 cells in the Mimosaceae and Caesalpiniaceae, usually of less than 11 cells in the Papilionaceae. Distinctly storied in most Papilionaceae, often with obtuse-angled gable-ends; sometimes storied in the Caesalpiniaceae, more rarely and more vaguely storied in the Mimosaceae. Strands very short in most Papilionaceae.

Rays. Mostly 2–5 cells wide in the Mimosaceae, always homogeneous and typically composed of small cells (less than 10 μ tang. diam.); similar rays occur in some Caesalpiniaceae and Papilionaceae but heterogeneous rays

occur in some genera of Caesalpiniaceae, and in still more genera of Papilionaceae; mostly 1–3 cells wide in the Caesalpiniaceae and Papilionaceae. Rays that are not distinctly storied usually exhibit echelon arrangement in the Mimosaceae and Caesalpiniaceae but not in the Papilionaceae.

Fibres not uncommonly septate in Mimosaceae and Caesalpiniaceae, rarely septate in Papilionaceae. **Intercellular canals** of the vertical type, both normal and traumatic, more common in the Caesalpiniaceae. **Anomalous structure** most common in the Papilionaceae.

PHYSIOLOGY

Certain of the Papilionaceae have provided subjects for physiological investigation in relation to their morphology or anatomical structure. Thus Boodle (234) demonstrated that the number of trifoliate seedlings of gorse (*Ulex europaeus* Linn.) was greater when grown on a rich soil than on sand. Warington (2361) showed how, in *Vicia faba* Linn., the absence of boron caused cambium cells to disintegrate with or without preliminary hypertrophy, the phloem and ground tissue to become disorganized, and the xylem to be poorly developed or even to break down. Kraus and Mitchell (1279) studied the effect of alpha-naphthalene acetamide on bean plants. They found that this chemical causes the root system to become more fibrous, whilst the initiation of roots from derivatives of ray cells is also stimulated. Vascular bundles were found to arise from proliferated endodermal cells. Nightingale and Farnham (1602) studied the effects of nutrient concentration on the anatomy, metabolism, and abscission of buds of the sweet pea, and Jenkins (1170) examined snap bean tissues affected with black rot.

ECONOMIC USES

The economic products obtained from the Papilionaceae are numerous. The most familiar are the various food-yielding plants such as the many kinds of peas and beans derived from species of *Arachis*, *Cajanus*, *Cicer*, *Dolichos*, *Glycine*, *Lens*, *Phaseolus*, *Vicia*, and the fodder plants including the vetches, lupins, lucernes, clovers, &c., derived from species of *Lupinus*, *Medicago*, *Melilotus*, *Onobrychis*, *Trifolium*. One of the best-known fibre plants is Sunn Hemp (*Crotalaria juncea* Linn.), but there are others of smaller or local importance such as the Spanish Broom (*Spartium junceum* Linn.). The blue dye indigo, obtained from species of *Indigofera*, was at one time a product of considerable importance. Gums are obtained from certain members of the family, notably Tragacanth from *Astragalus gummifer* Lab. and Sarcocolla from *A. sarcocolla* Dymock. Balsam of Tolu and Balsam of Peru, two oleoresins derived respectively from *Myroxylon balsamum* (Linn.) Harms and *M. balsamum* var. *pereirae*, are used in medicine and perfumery. In recent years the roots of various species of *Derris* and *Lonchocarpus* have assumed considerable importance as the source of insecticides, chiefly because of their content of rotenone and related substances. Numerous plants with alleged medicinal properties occur in the family, but few of them are of great importance except liquorice (*Glycyrrhiza glabra* Linn.).

The anatomical features of some of these economic products are important for purposes of identification. A selection is given on pp. 530–2.

TUBA ROOT (*Derris* spp.)

Roots up to 1 cm. in diameter with greyish-brown bark, with shallow, sinuous, longitudinal furrows. Older roots partly encircled by transverse ridges. Xylem, on a freshly cut transverse surface, cream to pale yellow; vessels easily visible except at the centre. Cork consisting of up to about 12 layers of cells; outer cells dark reddish-brown; inner ones lighter in colour and thin-walled. Groups of stone cells and numerous secretory cells with shining, golden-brown contents present beneath the cork. Phloem stratified into tangential zones of hard and soft tissue, and broken up into wedge-shaped strands with enlarged distal ends of the rays. Phloem fibres very thick-walled, average diameter about $10\ \mu$. Secretory cells, containing resin and rotenone, frequent between the groups of phloem fibres. Xylem including vessels of 2 distinct sizes. Larger vessels elliptical to circular in transverse section, diameter 110×90 – $210 \times 170\ \mu$, but usually about $180 \times 155\ \mu$, mostly solitary or occasionally accompanied by 1–6 much smaller angular vessels generally about $27 \times 32\ \mu$ in diameter. Small vessels also occur arranged in radial rows or clusters of 3–6. Vessel members mostly 140 – $190\ \mu$ long. Perforations simple. Pits alternate, elliptical to polygonal, about $6\ \mu$ broad, with horizontal, slit-like borders; distinctly vested. Ground tissue of the xylem consisting mostly of storied parenchymatous cells filled with starch, a few containing resin or rotenone. Compact strands of fibres occur in the parenchymatous ground-mass, each strand consisting of 2–50 very thick-walled elements about $10\ \mu$ in diameter and surrounded by a sheath of cells each containing a solitary crystal embedded in thickenings of the inner tangential walls. Rays homogeneous, 1–6 cells wide. (For another description of the root of *Derris elliptica* see Russell (1972).)

CUBE ROOT (*Lonchocarpus utilis* H. B. et K.)

Roots up to about 22 mm. in diameter, pale yellowish-brown, surface slightly furrowed longitudinally and provided with chocolate-brown, transversely elongated lenticels. Freshly cut transverse surface pale cream in colour, turning yellow when moistened with water. Cube roots can readily be distinguished from Tuba (*Derris*) by the much less numerous phloem fibres and by the relatively infrequent vessels, the latter being mostly solitary or in occasional radial or oblique pairs, seldom exceeding $33\ \mu$ in diameter except in a few specimens where they rarely attain up to about $180\ \mu$.

According to Panshin (1651) it is not always easy to identify a particular species of rotenone-yielding plant from its microscopical structure alone, for although differences in the size and frequency of the different elements of the secondary xylem are known to occur in closely related species, the variations are no greater than those which may be found in sections of the stem and roots taken from different parts of the same plant. Worsley (2473), after examining 22 species of Papilionaceae for the presence of rotenoids, found that these substances occur in varying amount in *Derris*, *Millettia*, *Mundulea*, and *Tephrosia*. He also concluded that rotenoids are waste products of the plant's metabolism except possibly in the seed. The structure of *Millettia* has been described by Russell (1973). For information concerning the taxonomy of plants which yield rotenoids see Krukoff and Smith (1290).

LIQUORICE (*Glycyrrhiza glabra* Linn. and related species of *Glycyrrhiza*)

The commercial product consists of the rhizome and root. It occurs in pieces 1–2 cm. in diameter. Surface reddish-brown when unpeeled, but the commercial product often has the outer tissues removed. The more important microscopical features include the very broad rays by which xylem is dissected into radiating groups; the cork consisting of up to about 15 layers of golden to chocolate-brown cells with thickened tangential walls; the strands of thick-walled fibres in the phloem and xylem, each strand usually approximately rectangular in transverse section and consisting of 10–50 but occasionally including as many as 100 members often accompanied or sheathed by cells each of which contains a prismatic crystal; the xylem vessels, either solitary or in small clusters, the individual members being 40–130 (mostly about 100) μ in diameter; the numerous starch grains mostly about 10 μ in diameter. Senft (2079) has described and discussed the physiological function of amorphous deposits in certain of the cells of *Glycyrrhiza glabra*.

BAPTISIA OR WILD INDIGO ROOT (*Baptisia tinctoria* R. Br.)

The woody rhizome and root are used in medicine as a laxative. The root contains 2- to 4-compound starch grains, lignified phloem fibres, and brownish cork cells. A rhizome and root, which had been substituted for those of *Baptisia tinctoria*, were provisionally identified at Kew as *Thermopsis* sp. For the anatomy of the root, stem, and leaf of *Baptisia tinctoria* see Holm (1030).

ANGELIM BARK (*Andira* and *Hymenolobium* sp.)

The anatomy of the so-called Angelim barks from Brazil, to which medicinal properties have been attributed, has been fully described (Brocardet 276).

PISCIDIA ERYTHRINA BARK

Jaeger (1140) has described the structure of the bark of *Piscidia erythrina* Lam., which is used to prepare fish poison. Characters mentioned as being of particular diagnostic value are the resin cavities in the cortical parenchyma, and the cells, in the same region, which contain bipyramidal quadratic crystals, partly or wholly embedded in a lignified deposit within the cells.

ADESMIA BORONIOIDES

Adesmia boronioides Hook. f. from Patagonia is a small shrub, 18 inches high, the leaves of which are covered with glands which secrete a viscid substance with a pleasant balsamic odour, which might be worthy of consideration for use in perfumery. The small, resin-covered leaflets, especially those of the young leaves when still not fully unfolded, have a characteristic appearance which, in specimens from which the typical, yellow, papilionaceous flowers are absent, might be mistaken at first sight for inflorescences. The stems are green when very young, but reddish-brown and longitudinally striated when slightly older. The microscopical features of the leaf include the infrequent, simple hairs, each having a few short basal cells and a long terminal cell; the approximately isobilateral mesophyll of the leaflets; the large masses of feathery crystals of unidentified material in the mesophyll (the material is dissolved during the preparation of balsam mounts); the glands embedded

in the outer part of the mesophyll; the deeply crescentic group of widely spaced vascular bundles, each supported externally by well-developed 'pericyclic' fibres, visible in transverse sections of the rachis. The microscopical features of the stem include the small glands in the outer part of the primary cortex; the large, broad, tangentially elongated strands of pericyclic fibres; the well-defined, primary vascular bundles with numerous vessels united by interfascicular fibres to form a closed ring; the broad pith; the occasional, elongated secretory cavities in the pith and cortex, those in the pith containing yellowish-brown material.

MUMMY PEA (*Pisum sativum* var.)

The structure of the so-called 'mummy pea' has been described by Compton (456). The 'mummy pea' is a variety of *Pisum sativum* Linn. in which the upper part of the axis is funnel-shaped and bears a dense cluster of leaves and short inflorescences. The following is a quotation from Compton's paper:

'In the uppermost region of the swollen funnel-shaped axis, two continuous concentric rings of vascular tissue are present. The outer of these rings is directly continuous with the single ring of bundles below, and the different vascular elements of the xylem, phloem, etc. have normal orientation. The inner ring on the other hand has an inverse orientation of tissues. In between the two rings of vascular bundles is found a zone of parenchymatous tissue, histologically like a medulla. No vascular connection was discovered between the bundles of the outer cylinder and those of the inner, either at the node at which the latter takes its origin, or at any point of its course.'

The structure is an example of ring fasciation and breeds true.

Other useful references to the microscopical structure of members of the Papilionaceae of economic importance include the following. Winton (2443) has described a method for the detection of lucerne (*Medicago sativa* Linn.), red clover (*Trifolium pratense* Linn.), and alsike clover (*T. hybridum* Linn.) when present in ground material used as cattle food. Anatomical details by which it is claimed that species of *Trifolium* may be distinguished from one another have been recorded by Vechot (2328). Articles dealing with the anatomy of *Arachis hypogaea* Linn. have been published by Waldron (2344) and Reed (1896), and on the Lima bean by Snell and Pollard (2155), on the coffee bean (*Cicer arietinum* Linn.) by Holm (1003), on the lupin by Boas and Merckenschlager (209), on the developmental anatomy of the root of *Melilotus alba* Desr. by Bottum (242), whilst further general information concerning leguminous crop plants may be found in the text-books of Hector (929) and Hayward (927).

The histology of *Astragalus molissimus* Torr., which, when eaten, causes the 'Loco' disease of cattle in Kansas, has been described by Ritter (1904), with a view to facilitating its identification in cattle food.

TIMBERS

This family produces a number of woods that have been known and prized throughout the world for a very long time; some of them are among the most valuable woods known for inlay and cabinet work, musical instruments, and carving.

The most important genus is *Dalbergia*, which is the source of the following important timbers: Rosewood, e.g. Brazilian Rosewood, *D. nigra* Fr. All., Honduras Rosewood, *D. stevensonii* Standl., and Indian Rosewood, *D. latifolia* Roxb., Cocobolo, *D. retusa* Hemsl., Tulipwood, *Dalbergia* sp., Kingwood, *D. cearensis* Ducke, and African Blackwood, *D. melanoxyton* Guill. et Perr. *Pterocarpus* also produces several well-known timbers such as Padauk, Narra, and Red Sanders. Among the other timbers of importance may be mentioned Angelim or Partridge Wood, *Andira inermis* (Sw.) H. B. et K., Cocus or Brown or Green Ebony, *Brya ebenus* DC., and Black Bean, *Castanospermum australe* A. Cunn.

Though most of the woods are hard, heavy, deeply coloured, and durable, the wood of the Ambatch tree, *Aeschynomene elaphroxylon* (Guill. et Perr.) Taub., lies at the other extreme, with an air-dry specific gravity of about 0.2.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abrus,* Adenocarpus,* Adesmia,* Aeschynomene, Alhagi, Alysicarpus, Amicia, Ammodendron, Amorpha, Amphicarpaea, Amphithalea, Anagyris, Anarthrophyllum, Andira, Anthyllis,* Aotus, Apios,* Apoplanesia, Arachis,* Argyrolobium, Aspalathus, Astragalus,* Atylosia, Baphia, Baptisia,* Barbiera, Borbonia, Bossiaea, Bowdichia, Brachysema, Brongniartia, Brya, Buchenroedera, Burtonia, Butea, Cajanus, Calophaca, Calopogonium, Calpurnia, Calycotome, Camposema, Canavalia, Caragana,* Carmichaelia,* Castanospermum,* Centrolobium, Centrosema, Chadsia, Chaetocalyx, Chapmannia, Chorzema,* Cicer,* Cladrastis,* Clathrotropis, Cleobulia, Clianthus, Clitoria, Cochlianthus, Coelidium, Cologania, Colutea,* Cordyla, Coronilla,* Corynella, Cranocarpus, Cratylia, Crotalaria,* Cyamopsis, Cyclopia, Cylista, Cymbosema, Cytisopsis, Cytisus,* Dalbergia,* Dalea, Dalhousiea, Daviesia, Derris,* Desmodium,* Dichilus, Dillwynia, Dioclea, Diphaca, Diphysa, Diplotropis, Dipteryx, Discolobium, Dolichos, Dorycnium, Drepanocarpus, Dumasia, Dunbaria, Ebenus, Eleiotis, Erinacea, Eriosema, Erythrina,* Euchlora, Euchresta, Eutaxia, Eversmannia, Eysenhardtia, Fagelia, Flemingia, Galactia, Galega,* Gastrolobium, Geissaspis, Genista,* Geoffraea, Glycine,* Glycyrrhiza,* Gompholobium, Goodia, Grona, Gueldenstaedtia, Halimodendron,* Hallia, Hammatolobium, Hardenbergia, Harpalyce, Hedysarum,* Helminthocarpum, Herminiera, Heylandia, Hippocrepis, Hosackia, Hovea, Hymenocarpus, Hypocalyptus, Indigofera,* Jacksonia, Kennedya, Lablab, Laburnum,* Lathriogyna, Lathyrus,* Latrobea, Lebeckia, Lens, Leptodesmia, Lespedeza,* Lessertia, Liparia, Loddigesia, Lonchocarpus,* Lotononis, Lotus,* Lourea, Lupinus,* Machaerium, Marina, Mecopus, Medicago,* Melilotus,* Millettia,* Mirbelia, Mucuna, Muellera, Mundulea, Myrospermum, Myroxylon,* Nissolia, Olneya, Onobrychis, Ononis,* Ormocarpum, Ormosia, Ornithopus, Ougeinia, Oxylodium,* Oxytropis,* Pachyrhizus, Parochetus, Periantra, Petalostemon, Petteria,* Phaseolus,* Phyllota, Phylloxylon, Physostigma, Pictetia, Piptanthus,* Piscidia, Pisum,* Platycyamus, Platylodium, Platymiscium, Platysprion,* Platypodium, Podalyria, Poecilanthe, Poirertia, Poitaea, Pongamia, Priestleya, Priotropis, Pseudarthria, Psophocarpus, Psoralea,* Pterocarpus, Pterodon, Pueraria, Pultenaea, Pycnospora,

Rafnia, Rhynchosia, Robinia,* Rothia, Rudolphia, Sabinea, Scorpiurus,* Securigera,* Sesbania, Shuteria, Smithia, Soemmeringia, Sophora,* Spartium,* Spatholobus, Sphaerolobium, Sphaerophysa,* Strongylodon, Stylosanthes, Sutherlandia, Swainsonia, Swartzia, Sweetia, Taverniera, Templetonia, Tephrosia, Teramnus, Tetragonolobus, Thermopsis,* Tipuana, Trifolium,* Trigonella,* Ulex,* Uraria, Viborgia, Vicia,* Vigna, Viminaria, Virgilia, Voandzeia, Wistaria,* Zollernia, Zornia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Aeschynomene, Afrormosia, Alexa, Amerimnon, Amherstia, Ammodendron, Amorpha, Anagyris, Andira, Apoplanesia, Ateleia, Baphia, Behaimia, Belairia, Benthamantha, Bergeronia, Bowdichia, Brya, Butea, Calycotome, Canavalia, (Cascaronia), Cashalia, Castanospermum, Centrolobium, Cladrastis, Clathrotropis, Coumarouna, Coursetia, Crotalaria, Cytisus, Dalbergia, Dalea, Daviesia, Derris, (Desmodium), Diphysa, Diplotropis, Dipteryx, Drepanocarpus, Dussia, Ecastophyllum, Erythrina, Etaballia, Eysenhardtia, Genista, Geoffraea, Gliricidia, Gourliea, Halimodendron, Haplormosia, Harpalyce, Hebestigma, Hymenolobium, (Ichthyomethia), Indigofera, Inocarpus, Kunstleria, Laburnum, Lennea, Lespedeza, Lonchocarpus, Lupinus, Machaerium, Medicago, Millettia, Monopteryx, (Mucuna), Muellera, Myrocarpus, Myrospermum, Myroxylon, Ormosia, Ostryocarpus, Ougeinia, (Pachyrhizus), Paramachaerium, Parosela, Pericopsis, Pickeringia, Piscidia, Platycyamus, Platymiscium, Platypodium, Podalyria, Poecilanthe, Pongamia, Pterocarpus, Pterodon, Pueraria, (Retama), Rhynchosia, Robinia, Rothia, Sabinea, (Sarothamnus), Schefflerodendron, Sesbania, Sophora, Spartium, Spatholobus, (Strongylodon), Swartzia, Sweetia, Tipuana, Toluifera, Torresia, Ulex, Virgilia, Vouacapoua, Wistaria.

LITERATURE

(i) On General Anatomy

Alexandrov 12, Anonymous 28, Beijer 168, Boas and Merckenschlager 209, Boer 214, Bombacioni 223, Bond, G. 226, Boodle 234, Bottum 242, Bowman 250, Brocardet 276, Buchegger 303, Buder 305, Compton 456, Dastur and Saxton 542, Dormer 601, 602, 604, 605, Dubard and Dop 611, Evenari (Schwarz) 665, Fehér 680, 681, George 756, Goodlatte 795, Gravis 804, Hagerup 864, Handa 882a, Hayward 927, Hector 929, Hill, T. G. 973, Holm 993, 1003, 1030, Hunter 1111, Jacobsohn-Stiasny 1137, Jaeger 1140, Jenkins 1170, Jimbo 1181, Jolivet 1187, Kraus and Mitchell 1279, Krukoff 1289, Krukoff and Smith 1290, Lacoste 1311, 1312, Leupin 1364, Lindemuth 1373, Löw 1397, Manganaro 1431, Metcalfe 1494, Morvillez 1560, Nightingale and Farnham 1602, Panshin 1651, Parsa 1657, Pellegrin 1682, Reed 1896, Reeve 1901, Ritter 1940, Russell 1972, 1973, Sabnis 1977, Schilling 2032, Senft 2079, Severini 2080, Skipper 2119, Smith and Kersten 2149, Snell and Pollard 2155, Staber 2178, Starr 2188, Taylor 2239, Vechot 2328, Waldron 2344, Walensky 2345, Ward, H. M. 2360, Warrington 2361, Watari 2364, Winter 2442, Winton 2443, Worsley 2473, Zemke 2505, Ziegenspeck 2506.

(ii) On Wood Structure

Bailey 78, Beekman 167, Beijer 168, Benoist 170, den Berger and Endert 183, Besson 186, Bienfait and Pfeiffer 197, Brit. Hond. For. Dept. 274, Brown, F. B. H. 282, Brown, H. P. and Panshin 288, 289, Burgerstein 310, 312, Chalk and Chattaway 362, Chalk *et al.* 363, 364, Chalk and Rendle 365, Chowdhury 411, 415, Cooper and Record 461, Coster 481, Cozzo 494, Dadswell and Eckersley 525, Descole and O'Donnell 576, Dixon 592, Ewald 666, Foxworthy 705, Gregus 2532, Hess 960, Hopkinson 1083, Howard 1088, Janssonia 1147, 1154, Janssonius and Moll 1156, Jentsch 1177, Jolly 1188, Jones 1191, Kanehira 1206, 1209, 1213, Kanehira *et al.* 1214, Kribs 1283, Lecomte 1334, Leonhardt

and Fay 1360, Martin-Levigne 1450, Méniaud 1492, Messeri 1493, Metcalfe 1497, Miller 1537, Normand 1615, Panshin 1651, Pearson and Brown 1679, Pereira 1687, Record 1783, 1788, 1836, 1841, 1843, 1846, 1850, 1851, 1862, 1863, 1883, Record and Hess 1886, Record and Mell 1894, Riera 1937, Scott 2075, Stevenson 2199, Stone 2202, 2203, 2206, 2207, Tang 2230, 2231, Torres 2269, Tortorelli 2273, Uspensky 2317, Wallis 2348, Williams 2430.

116. KRAMERiaceae

(FIG. 118 on p. 536)

SUMMARY

A small family of shrubs, ranging from Mexico to Chile, which comprises the single genus *Krameria*. The shape of the leaf or leaflet, as seen in transverse sections, varies considerably in different species, and might well prove to be of considerable diagnostic value. The outer walls of the epidermal cells of the lamina are usually heavily cutinized. **Hairs**, which vary in frequency and length and occur on the leaves and young twigs, are invariably thick-walled and unicellular. **Stomata** are present on both surfaces of the leaf, whilst the mesophyll includes clusters of sclerosed, pitted, parenchymatous cells at the centre. **Cork** in the young stem usually arises in the inner part of the cortex or pericycle, and, in some species, cuts off the large strands of fibres which occur in the **pericycle**. The **xylem** in young twigs forms a continuous cylinder traversed by narrow rays. The vessels are invariably small, but infrequent to numerous in different species. The hard ground tissue of the wood is composed of fibres with bordered pits. The diameter of the **pith** varies considerably in different species. Cluster **crystals** are common in the parenchymatous tissues, whilst **secretory cells**, with presumably tanniniferous contents, are common.

LEAF

Lamina of the leaf or leaflet varying in shape in different species; isobilateral in the species with a relatively large lamina, e.g. *K. argentea* Mart., *K. lanceolata* Torr., and *K. tomentosa* St. Hil., but centric in smaller leaves, e.g. in *K. parvifolia* Benth. (Fig. 118 K). **Hairs** invariably unicellular, thick-walled, but varying in length and frequency in different species, e.g. very numerous in *K. greyi* Rose et Painter, relatively short and infrequent in *K. cistoidea* Hook. Outer walls of the cells of the **epidermis** strongly cutinized; usually arched outwards and sometimes tending to be papillose. **Stomata** present on both surfaces; those of *K. tomentosa* (Fig. 118 M) usually surrounded by 4–6 cells slightly differentiated from the remainder of the epidermis, 2 of the surrounding cells being commonly but not invariably parallel to the pore. Stomata not examined at Kew in surface view for other species, but said by Kunz (1306) to be mostly rubiaceous and variously orientated in other species as well. **Mesophyll**. Usually with a single layer of palisade cells towards both surfaces and at the margins; 2 palisade layers observed in *K. cistoidea* Cav. and *K. triandra* Ruiz. et Pav. but palisade tissue not very well defined in the last of these species. Centre of the mesophyll consisting of somewhat spongy tissue, including, in all species examined except *K. paucifolia* DC., small clusters of thick-walled, pitted, sclerosed cells. Vascular bundles of the **veins** embedded in the mesophyll, each supported by small groups of

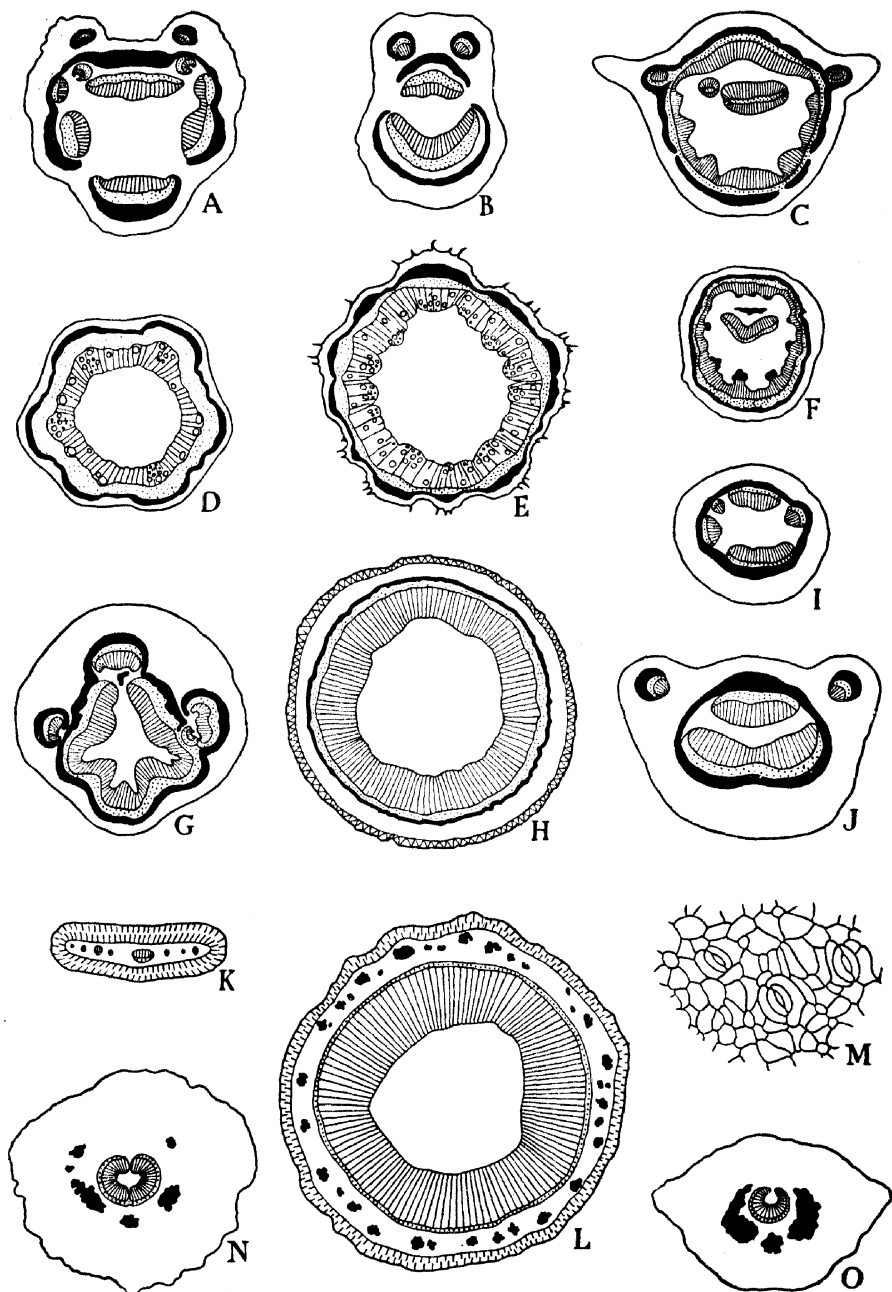


FIG. 118. **LEGUMINOSAE—MIMOSAACEAE, A-E; LEGUMINOSAE—CAESALPINIACEAE, F-J; KRAMERIACEAE, K-O**

A, *Acacia decurrens* Willd. var. *dealbata* F. Muell. Petiole $\times 11$. B, '*Prosopis jacari* Hort.'. Petiole $\times 32$. C, *Inga punctata* Willd. Petiole $\times 18$. D, *Entada scandens* Benth. Stem $\times 12$. E, *Acacia decurrens* Willd. var. *dealbata* F. Muell. Stem $\times 7$. F, *Saraca declinata* Miq. Petiole $\times 10$. G, *Brownnea coccinea* Jacq. Petiole $\times 13$. H, *Haematoxylon campechianum* Linn. Young stem $\times 53$. I, *Gymnocladus dioica* K. Koch. Stem $\times 6$. J, *Bauhinia forficata* Link. Petiole $\times 32$. K, *Krameria parviflora* Benth. T.S. Leaflet $\times 18$. L, *K. ixina* Linn. Stem $\times 18$. M, *K. tomentosa* A. St. Hil. Leaf epidermis $\times 100$. N, *K. tomentosa* A. St. Hil. Petiole $\times 28$. O, *K. argentea* Mart. Petiole $\times 33$.

thick-walled fibres, but the amount and arrangement of the fibres varying in different species. Transverse sections through the distal end of the **petiole** of *K. argentea* (Fig. 118 O) exhibit a small crescent-shaped vascular strand with very much incurved ends (almost cylindrical), supported by large columns of pericyclic fibres; structure similar but with less supporting fibres in *K. tomentosa* (Fig. 118 N); vascular arc more open and not supported by pericyclic sclerenchyma in *K. cistoidea*; main vascular strand with a cylinder of xylem accompanied by a crescent of phloem and supported by a broad arc of very thick-walled fibres in *K. ixina* Linn. Very small additional strands towards the wings present in some species. Cluster **crystals** common in all unligified tissues of the leaf of most species, but varying in frequency; sphero-crystals seen in the mesophyll of *K. cistoidea* and *K. triandra*; crystal-sand recorded by Kunz (1306) in certain species. **Secretory cells** with amorphous, probably tanniniferous, contents common in the mesophyll and petiole.

AXIS

YOUNG STEM (Fig. 118 L)

Epidermis composed of cells with thickly cutinized outer walls; cells in some species arched outwards or even tending to be papillose. Outer part of the primary **cortex** differentiated as palisade tissue in *K. argentea* Mart., *K. cistoidea* Hook. (not very well differentiated), *K. greyi* Rose et Painter, *K. ixina* Linn., and *K. tomentosa* St. Hil. Definite palisade tissue not observed in the other species examined. Inner part of the cortex in all species parenchymatous. **Cork** generally arising fairly deep in the cortex or even in the pericycle, the pericyclic fibres being cut off when the cork is sufficiently deep seated; composed of cells which are thin-walled apart from the suberized outer walls which are thicker and dome-shaped. **Pericycle** usually including isolated, but in some species large, strands of thick-walled fibres. **Phloem** devoid of lignified elements in the material examined. **Xylem** in the form of a broad or narrow continuous cylinder, traversed by inconspicuous rays. Vessels varying in size, frequency, and arrangement in different species; up to 30 μ in radial diameter and mostly in radial groups in *K. argentea*; smaller and less numerous in *K. cistoidea*; infrequent, mostly solitary, radial diameter seldom more than 25 μ in *K. parvifolia* Benth.; numerous, up to about 45 μ in radial diameter in *K. tomentosa*; mostly solitary, but locally tending to be in radial chains, radial diameter seldom attaining 30 μ in *K. triandra* Ruiz. et Pav.; with spiral thickening or bordered pits and simple perforations in all of the species examined. Moderately to very thick-walled fibres with bordered pits form the ground tissue of the xylem in all species. **Pith** varying considerably in diameter in different species, e.g. broad in *K. argentea*, small in *K. parvifolia*; in most instances composed of or including a high proportion of moderately thick-walled, pitted cells. Clustered **crystals** present in all species; sphero-crystals as well as other clustered types observed in *K. cistoidea*, and *K. triandra*. A small proportion of the crystals contained in sclerenchymatous idioblasts in *K. greyi*, *K. ixina*, and *K. parvifolia*. Scattered **secretory cells**, with amorphous contents believed to be tanniniferous, occur in unligified tissues, but vary in frequency in different species.

ROOT, see 'Economic Uses' below

TAXONOMIC NOTES

Krameria has been variously assigned to the Polygalaceae or to the Leguminosae-Caesalpinziaceae. The taxonomic position of the genus is fully discussed by Kunz (1906) who took both anatomical and exomorphic evidence into consideration. He concluded that *Krameria* has no very close affinities with either of the above groups, and favoured the idea that it should form the basis of a distinct family.

ECONOMIC USES

Rhatany, used in medicine as an astringent, consists of the crown and larger roots of *K. triandra* Ruiz. et Pav. The roots are reddish, usually straight but sometimes slightly tortuous, mostly about the thickness of a finger, but attaining a diameter of 3 cm. or more near the crown. They have a somewhat irregular, slightly fibrous fracture, and the bark is easily detached from the xylem which occupies about two-thirds of the diameter. Microscopical features include the following. Cork narrow, consisting of about 8 layers of cells, only the outer tangential walls being thickened and dome-shaped; some of the cork cells filled with yellowish-brown contents. Primary cortex in the commercial article usually absent, having been cast off by the activity of the phellogen. Secondary cortex fairly narrow, composed of thin-walled parenchyma. Phloem in the form of elongated, triangular strands exhibiting outwardly directed, somewhat sinuous apices in transverse sections, including a high proportion of thick-walled, unlignified fibres with the lumina variously shaped and often slit-like. Phloem strands separated from one another by the expanded distal ends of the medullary rays. Vessels of the xylem numerous, arranged in approximately concentric circles, circular to oval, usually solitary and up to about 45 μ or more in radial diameter, with bordered pits having horizontal apertures; perforations simple. Ground-tissue of the wood composed of thick-walled fibres with conspicuous, bordered pits. Wood parenchyma arranged in slightly interrupted, uniseriate, concentric bands. Numerous, mostly simple but sometimes loosely compound, variously shaped starch grains present in the parenchymatous tissues. Solitary crystals and crystal-sand sometimes present in association with the phloem fibres.

GENUS DESCRIBED

Krameria.*

* The above description is based mainly on sections, now in the Kew slide collection, from herbarium specimens of the following species: *K. argentea* Mart., *K. cistoidea* Hook., *K. cytisoides* Cav., *K. greyi* Rose et Painter, *K. ixina* Linn., *K. lanceolata* Torr., *K. parvifolia* Benth., *K. paucifolia* DC., *K. tomentosa* St. Hil., *K. triandra* R. et P.

LITERATURE

On General Anatomy

Kunz 1906.

117. ROSACEAE (EXCLUDING CHRYSOBALANOIDEAE)

(FIG. 119 on p. 542; FIG. 120 on p. 544)

SUMMARY

(i) GENERAL

Trees, shrubs, or herbs with very few anatomical features common to the whole family. The family is very widely distributed but many species occur in north temperate regions. **Hairs** generally unicellular, in the form of simple trichomes, or occasionally united to form tufts. Glandular hairs, and glandular shaggy hairs also occur. **Nectaries** are present on the petiole, leaf surface, and on the leaf teeth in certain species. **Stomata** are ranunculaceous. **Cork** in the young stem arises superficially in some species but endogenously in others. **Pericycle** with strands of sclerenchyma or a continuous sclerenchymatous ring. The **vascular bundles** in the young stem are separated by very narrow medullary rays in some genera, so that the xylem appears in transverse sections to form a continuous ring around the pith. In other genera the bundles are widely separated by broad primary rays and therefore appear as individually distinct units. Calcium oxalate is usually secreted in the form of solitary or clustered **crystals**. True styloids are known only in *Quillaja*. **Secretory elements**. Mucilaginous cells are common in the leaf epidermis and in the parenchyma of the leaf veins and stem (*Eriobotrya* and *Neurada*); lysigenous mucilage canals also occur in the pith of *Neurada*. Tannin is abundant but not usually localized in special cells.

Characters such as the outline of the epidermal cells as seen in surface view; the structure of the stomata; the number of palisade layers; the size, nature, and distribution of crystals; the structure of the larger vascular bundles; the nature and size of the hairs have been employed by Gyhr (854) for the microscopical identification of the leaves of members of the Rosaceae with medicinal properties. These characters are, however, of value only for specific and to a certain extent for generic diagnosis. No satisfactory leaf characters for the separation of the tribes were found by Gyhr, but, on the other hand, it was much easier to divide the leaves into two classes according to whether they were from herbaceous or woody plants.

When making use of the outline of the epidermal cells as seen in surface view for diagnostic purposes, it would be as well to bear in mind the variations in this character which were found by Haberlandt (859) in sun and shade leaves of an individual species during his researches on the *Crataegomespili*. Minor variations between mesophytic and dune forms of *Prunus* (Starr 2188) and between sun and shade leaves of *Rubus* spp. (Bird 199) have also been recorded. Variations in the stem structure which may occur within an individual species of *Crataegus*, *Prunus*, or *Pyrus* have also been described by Aubertot (48).

(ii) Wood

Vessels in temperate species mostly small and numerous, with a tendency to ring-porousness, with oblique or radial arrangement in some species, often spirally thickened, perforations typically simple, but with sporadic multiperforate plates in some species, intervascular pitting alternate, small, pits to

parenchyma similar; members of medium length. **Parenchyma** typically apotracheal, diffuse or in short bands, with some scanty paratracheal parenchyma in a few species. **Rays** mostly 2-5 cells wide, considerably more in some genera and occasionally of 2 distinct widths; heterogeneous to homogeneous. **Fibres** typically with numerous distinctly bordered pits on radial and tangential walls, of medium length to moderately long.

LEAF

Usually dorsiventral. Centric in *Crataegus azarolus* Linn. **Hairs** commonly unicellular but showing considerable variations in structure. (i) With characteristic, solid, wart-like projections in *Kerria* and *Neviusa*. (ii) Forming tufted or stellate groups in species of *Potentilla* (section *Stelligerae*), certain *Rubus* spp., and *Spiraea sorbifolia* A. Br. Stalked capitate glands occur in *Alchemilla*, *Fragaria*, *Geum*, *Potentilla*, *Prunus*, *Rosa*, *Rubus*, and *Sanguisorba*. Non-capitate, multicellular hairs also recorded by Gyhr (854) in *Sanguisorba*. **Spines** of *Rosa* and *Rubus* arise superficially. **Nectaries** on the petiole of certain species of *Prunus* are stated by Gregory (815) and Knapheisowna (1249) to contain sugar and tannin, and, according to Dorsey and Weiss (607), to represent the suppressed members of an originally ternate leaf. Glandular leaf teeth recorded in *Crataegus*, *Cydonia*, *Pyrus*, *Sorbus*, and secretory leaf teeth, devoid of palisade epidermis, in *Alchemilla*, *Fragaria*, *Kerria*, *Rubus*, *Sanguisorba*, *Spiraea*. Glandular spots present on the lower surface of the leaf of *Laurocerasus*, and oil drops in the palisade cells of *Prunus laurocerasus* Linn. **Cuticle** striated in *Chaenomeles japonica* Lindl. Elevations of cuticle around the stomata recorded in *Pyrus communis* Linn. Cells of the **epidermis** varying in outline as seen in surface view; provided with a stratified coating of wax in *Kerria japonica* DC. Lower epidermis papillose in certain species of *Amelanchier*, *Cotoneaster*, *Prunus*, *Pyrus*, *Rosa rugosa* Thunb., *Sorbus*, and *Spiraea*. Papillose on both surfaces in *Acaena adscendens* Vahl. Inner walls on the epidermal cells commonly mucilaginous. Variations in the gelatinization in different species of *Cliffortia* have been described by Montcheff (1553). **Hypoderm** occurs in certain species of *Heteromeles*, *Osteomeles*, *Pygeum*, *Rubus* (section *micranthobatus*), and *Sibiraea*. **Stomata** nearly always confined to the lower surface, except in *Geum parviflorum* Sm. (Betts 190), *Neurada procumbens* Linn. (Sabnis 1977), and *Rosa berberifolia* Pal. (syn. *persica* Michx.?). Stomata situated in pits in *Cliffortia* (Montcheff 1553). **Hydathodes** present in the leaf teeth of *Agrimonia*, *Alchemilla*, *Crataegus*, *Geum*, *Potentilla*, and possibly other genera (see also under 'Glands'). **Mesophyll** generally with 2 or more layers of palisade cells, but 1 single layer recorded by Gyhr (854) in certain species of *Alchemilla* and *Geum*. Normal palisade stated to be absent from *Prunus armeniaca* Linn. Mesophyll consisting wholly of short palisade cells in *Neurada procumbens* (Sabnis 1977). **Vascular bundles** of the smaller veins with or without sclerenchyma in the parenchymatous sheath surrounding them; vertically transcurrent in *Neurada procumbens* (Sabnis 1977). **Petiole** exhibiting the following types of structure in transverse sections through the distal end. (i) An arc of vascular bundles in *Acaena* (Morvillez 1556), *Agrimonia* (Fig. 119 F), *Filipendula* (Fig. 119 B), *Fragaria*, *Geum*, *Potentilla* (Morvillez 1556), *Poterium* (Fig. 119 D), *Prunus* (pro parte), *Quillaja*, *Raphiolepis*, *Rosa* (pro parte), *Rubus* (Betts 189), (Holm

1045), (Morvillez 1556), *Sanguisorba*, *Sorbus* (Morvillez 1556), *Spiraea* (sections *aruncus* and *sorbaria*) (Morvillez 1556), and *Waldsteinia* (Morvillez 1556). (ii) A solitary crescent-shaped bundle in certain species of *Amelanchier*, *Cotoneaster*, *Crataegomespilus*, *Cydonia*, *Dichotomanthes*, *Neviusa*, *Prunus* (Fig. 119 A) (pro parte and not including *Laurocerasus*), *Pyracantha*, *Pyrus* (pro parte) (Fig. 119 E), *Spiraea* (section *Holodiscus*) (Morvillez 1556). (iii) A principal solitary crescent-shaped bundle, accompanied by smaller or very small subsidiary ones in or towards the wings, in certain species of *Crataegus*, *Eriobotrya*, *Kerria*, *Neillia*, *Photinia*, *Potentilla* (Fig. 119 I) (pro parte) (Morvillez 1556), *Prunus* (including *P. laurocerasus*), *Pyrus* (pro parte), *Raphiolepis*, *Sorbus* (Fig. 119 G), *Stranvaesia*. (iv) Several centric bundles, each surrounded by an endodermis and consisting of a ring of xylem and phloem enclosing a pith-like tissue, in at least some species of *Alchemilla* (Fig. 119 C). (v) With 8-9 bundles, 1 being centric in structure as in *Alchemilla*, the remainder being hemicentric, each then consisting of an arc of xylem and phloem surrounded by an endodermis in '*Sanguisorba canadensis* Linn.'. The principal strand of *Eriobotrya japonica* Lindl. (Fig. 119 H) also centric (Morvillez 1556).

The *Crataegomespili*, or graft hybrids between *Mespilus germanica* Linn. and *Crataegus monogyna* Jacq., exhibit a proportion of characters which are intermediate between those of the parents but also exhibit a mosaic-like combination of parental characters. See Haberlandt (858, 859, 860, 861) and Weiss (2391).

Calcium oxalate generally present in the form of solitary or clustered **crystals**. True styloids recorded only in *Quillaja*. The type of crystal is sometimes characteristic of groups of species, e.g. (i) Crystals simple, or in clusters consisting of 3-4 components in *Rubus*, section *Micranthobatus*. (ii) Crystals exclusively clustered in *Rubus* sections, *Anoplobatus*, *Bathothammus*, *Eubatus*, *Idaebatus*. Exclusively or predominantly clustered crystals occur in *Potentilla* and *Spiraea*, and specially large rosette crystals in the petiole of species of *Prunus*, excluding *P. laurocerasus*. Crystals stated by Gyhr (854) to be absent from the leaf of *Mespilus germanica*.

AXIS

YOUNG STEM (Fig. 119 J-O)

Cork originating in very different positions in various members of the family, ranging from the epidermis or sub-epidermis in some species to the pericyclic region in others. Cork cells variable in structure. Mostly cubical with thin walls and tending to separate into concentric layers in *Neillia sinensis* Oliv. **Cortex**. Inner portion frequently collenchymatous in woody species; occasionally containing groups of stone cells in *Osteomeles* and *Pyrus*, and fibres in *Crataegomespilus*. Mucilage cells observed in the broad primary cortex of *Eriobotrya japonica* Lindl., and recorded by Sabnis (1977) in the cortex, rays, and pith of *Neurada procumbens* Linn. Palisade chlorenchyma present in the cortex of *Prinsepia*. **Endodermis** well defined in species of *Alchemilla*, *Fragaria*, *Gillenia* (Holm 1028), *Kerria*, *Neviusa*, *Potentilla* (Priestley and Hinchliff 1751), *Poterium*, and certain *Rubus* spp. (Betts 189). **Pericycle** of woody genera initially provided with primary bundles of fibres, but groups of stone cells subsequently develop between them to form a broken ring in certain species of *Chaenomeles*, *Crataegus*, *Osteomeles*, *Sorbus*, and

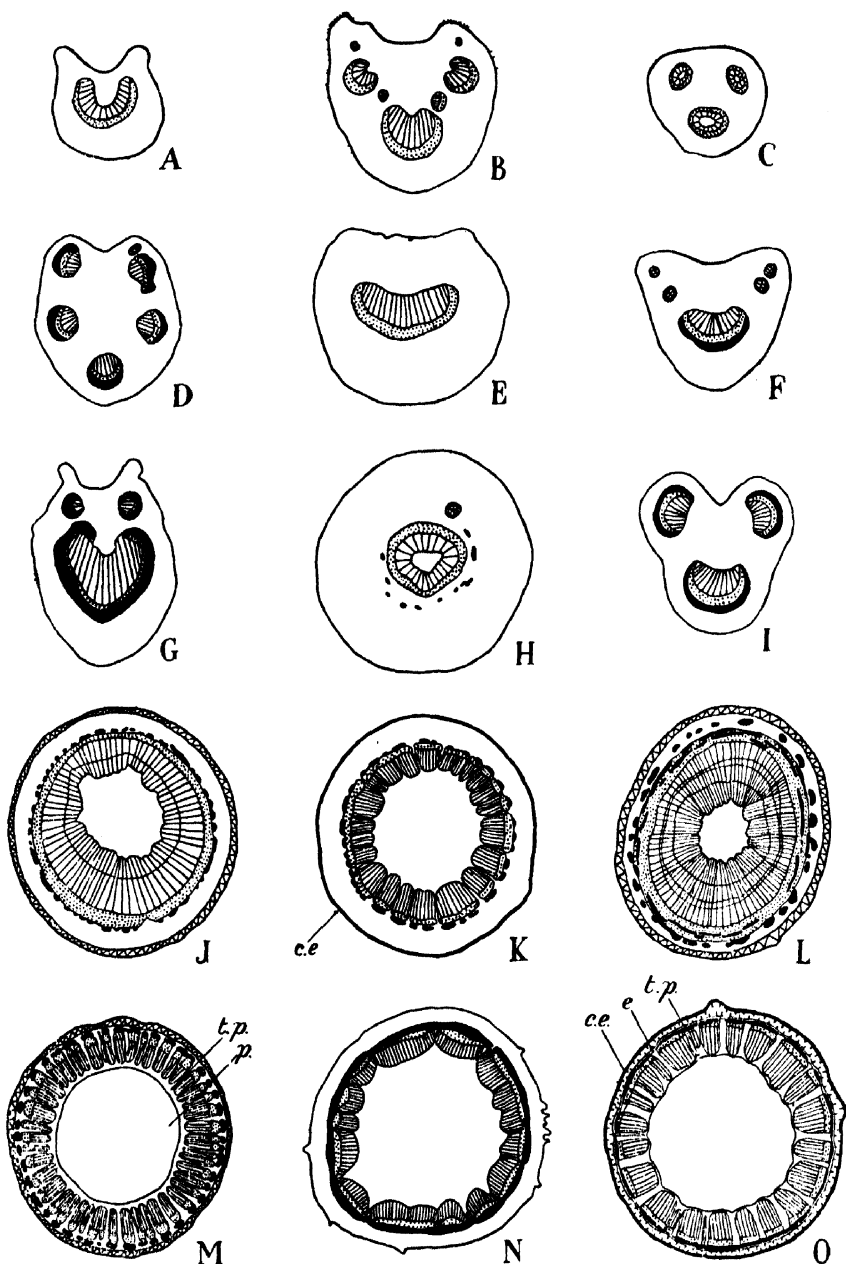


FIG. 119. ROSACEAE

A, *Prunus persica* Batsch. Petiole $\times 10$. B, *Filipendula ulmaria* (L.) Maxim. Petiole $\times 9$. C, *Alchemilla vulgaris* agg. Linn. Petiole $\times 10$. D, *Poterium officinalis* A. Gray. Petiole $\times 9$. E, *Pyrus communis* Linn. Petiole $\times 26$. F, *Agrimonia eupatoria* Linn. Petiole $\times 10$. G, *Sorbus aucuparia* Linn. Petiole $\times 13$. H, *Eriobotrya japonica* Lindl. Petiole $\times 6$. I, *Potentilla rupestris* Linn. Petiole $\times 13$. J, *Raphiolepis umbellata* Mak. Stem $\times 8$. K, *Rosa canina* Linn. Stem $\times 9$. L, *Cotoneaster frigida* Wall. Stem $\times 6$. M, *Rubus deliciosus* Torr. Stem $\times 9$. N, *Agrimonia eupatoria* Linn. Stem $\times 9$. O, *Kerria japonica* DC. Stem $\times 9$.

c.e. Cutinized epidermis. e. Endodermis. p. Thin-walled pith cells. t.p. Thickened pith cells.

Stranvaesia. Isolated strands of fibres with intervening unligified parenchyma present in certain species of *Amelanchier*, *Cotoneaster*, *Crataegomespilus*, *Crataegus*, *Cydonia*, *Dichotomanthes*, *Eriobotrya*, *Kageneckia*, *Kerria* (Bowman 250), *Lindleya*, *Neviusa*, *Osteomeles*, *Photinia*, *Potentilla*, *Poterium*, *Prinsepia*, *Prunus*, *Pygeum*, *Pyracantha*, *Pyrus*, *Quillaja*, *Raphiolepis*, *Rosa*, *Rubus*, *Sorbus*, *Stranvaesia*, and *Vauquelinia*. Pericyclic sclerenchyma absent from *Neurada procumbens* according to Sabnis (1977). Sclerenchymatous ring continuous in at least some of the species of *Agrimonia*, *Alchemilla*, *Fragaria*, *Geum*, *Kerria*, *Potentilla*; and practically continuous in British species of *Filipendula*. **Vascular bundles** separated by narrow primary rays, giving the xylem the appearance of a closed ring in at least some of the species of *Agrimonia*, *Alchemilla*, *Cotoneaster* (Fig. 119 L), *Crataegomespilus*, *Crataegus*, *Cydonia*, *Eriobotrya*, *Potentilla*, *Prunus*, *Pyracantha*, *Pyrus*, *Raphiolepis* (Fig. 119 J), *Rosa* (pro parte), and *Stranvaesia*. Vascular bundles sufficiently separated by the primary rays to be clearly visible as distinct units in at least some of the species of *Agrimonia* (Fig. 119 N), *Amelanchier*, *Cotoneaster*, *Fragaria*, *Geum*, *Gillenia* (Holm 1028), *Kerria* (Fig. 119 O), *Neviusa*, *Potentilla*, *Poterium*, *Rosa* (Fig. 119 K) (pro parte), *Rubus* (Fig. 119 M), and British species of *Filipendula*. Rays somewhat twisted in appearance where traversing the phloem as seen in transverse sections of certain species of *Prunus* and *Pyrus*. Vessels usually with simple perforations; reticulate plates occasional. Fibres recorded in the secondary **phloem** in species of *Cotoneaster*, *Crataegus*, *Cydonia*, *Mespilus*, *Pyrus*, *Rosa*, *Sorbus*, and *Spiraea*. **Pith** homogeneous in *Amelanchier*, *Cydonia*, *Eriobotrya*, *Neurada procumbens* (Sabnis 1977), *Pyrus communis* Linn., and heterogeneous in species of *Crataegus*, *Mespilus*, *Rosa*, *Rubus* (Holm 1045), *Sorbus*, *Spiraea*, and *Malus pumila* Mill.; septate in *Prinsepia*, and becoming hollow in certain species of *Geum*, and in the British species of *Filipendula*; very clearly differentiated into a thick-walled perimedullary portion and a central region consisting of much larger cells with thin walls in *Kerria japonica* DC., *Neillia sinensis*, and *Rubus deliciosus* Torr. For **crystals** see also 'Leaf'. Noteworthy types include the large rosette crystals in the primary cortex of species of *Prunus* (excluding *P. laurocerasus* Linn.), *Rosa hugonis* Hemsl., *Rosa* var. 'Dorothy Perkins', in the pericycle of *Rubus deliciosus*, and in the pith of *Malus pumila*, and *Rosa hugonis*. Solitary crystals in special cells have been reported amongst the phloem fibres of *Pyrus communis* and *P. nivalis* Jacq. as well as in the pericycle of *Eriobotrya japonica*. **Tannin** very common, especially in parenchymatous tissues. The arrangement of the tannin cells in the pith of *Rubus* has been used for taxonomic purposes, according to Solereder. **Mucilage canals** recorded in the pith of *Neurada* sp.

SPECIAL FEATURES

The mechanical elements are less well developed in 'weeping' than in erect forms of *Sorbus aucuparia* Linn., but according to Löw (1397) the differences are not very well defined.

Anatomical differences between the stems of 'American Pillar' and 'Dorothy Perkins' roses have been described in detail by Carlson (342).

The secretion of gum in *Prunus* may be sufficiently stimulated by parasitic organisms or physiological disturbances to constitute a serious disease of

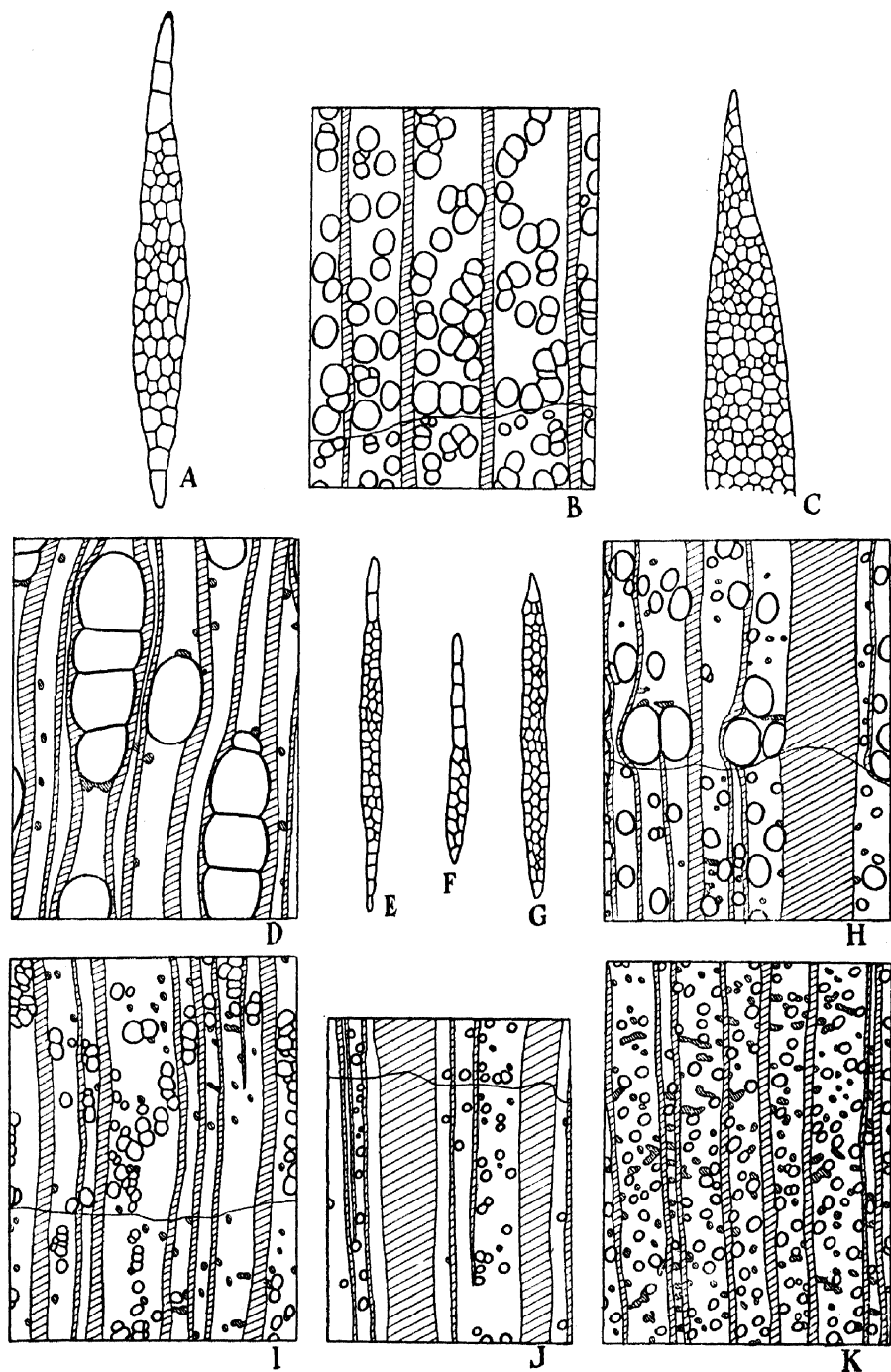


FIG. 120. ROSACEAE

A, *Prunus lusitanica* Linn. B, *P. avium* Linn. C, *Rosa canina* Linn. D, *Pygeum africanum* Hook. f. E, *Prunus maackii* Rupr. F, *Cotoneaster microphylla* Wall. G, *Prunus avium* Linn. H, *Rosa canina* Linn. I, *Prunus laurocerasus* Linn. J, *Spiraea alpina* Pall. K, *Raphiolepis umbellata* Mak. var.

fruit-trees. The formation of these gum deposits has been described by Butler (324).

The abscission of flowers or immature fruits of the apple has been studied by McCown (1464). Although there is a constriction zone in the pedicels of flowers and this persists during the life of the apple fruits, it plays no part in the abscission of flowers or fruits. Before flowers or fruits fall off, a definite abscission layer is formed. It is initiated independently in the pith and cortex. The **developmental anatomy** of the stem apex of the almond (*Prunus amygdalus* Batsch.) has been described by Brooks (278).

BARK

For anatomy of the bark of *Quillaja saponaria* Mol. see 'Economic Uses' on p. 548.

WOOD (Fig. 120)

Vessels typically small, mean tangential diameter less than 100 μ , except in some tropical species, often very small (25–50 μ), moderately large (200–300 μ) in *Eriobotrya*, *Hagenia*, *Laurocerasus* p.p., *Pygeum*, and *Rubus*; exclusively solitary or nearly so in the Pomoideae (except *Osteomeles*), *Amelanchier*, *Cotoneaster*, *Crataegus*, *Cydonia*, *Eriobotrya*, *Eriolobus*, *Malus*, *Mespilus*, *Micromeles*, *Photinia*, *Pourthiaea*, *Pseudocydonia*, *Pyrus*, and *Raphiolepis*; in some Rosoideae, *Cercocarpus*, *Chamaebatia*, and *Purshia*, and in *Quillaja* (Spiraeoideae); with radial and oblique arrangement or pore multiples of 4 or over in the Prunoideae, *Laurocerasus*, *Nuttallia*, *Padus*, *Prunus* (Fig. 120 1), and *Pygeum*, and producing a flame-like pattern in *Prunus ilicifolia* (Nutt.) Walp. (1886), in occasional clusters in *Hagenia*, *Laurocerasus*, *Padus* p.p., *Rubus* p.p.; typically very numerous (40 per sq. mm.), except where the vessels are large, between 30 and 40 per sq. mm. in *Holodiscus*, *Photinia*, *Pygeum*, and *Rubus* p.p., between 5 and 20 per sq. mm. in *Hagenia* and *Laurocerasus* p.p.; ring-porous or semi-ring-porous in some species of *Amelanchier*, *Cercocarpus*, *Chamaebatia*, *Cotoneaster*, *Fallugia*, *Holodiscus*, *Laurocerasus*, *Lyonothamnus* (1886), *Nuttallia*, *Opulaster* (2261), *Padus*, *Photinia*, *Physocarpus*, *Prunus*, *Purshia*, *Quillaja*, *Rosa*, *Sorbus*, *Spiraea*, and *Vauquelinia* (1886); spiral thickening occurs in about two-thirds of the genera examined and is present in most species of *Amelanchier*, *Cercocarpus*, *Chaenomeles*, *Chamaebatia*, *Cliffortia*,¹ *Cotoneaster*, *Crataegus*, *Cydonia*,² *Eriobotrya*, *Exochorda*, *Heteromeles*, *Kageneckia*, *Laurocerasus*, *Lyonothamnus*, *Malus*, *Mespilus*, *Nuttallia*, *Osteomeles*, *Padus*, *Photinia*, *Polylepis*, *Pourthiaea*, *Prinsepia* (1206), *Prunus*, *Pseudocydonia*, *Purshia*, *Pyrus*, *Raphiolepis*, *Rosa*, *Sorbus*, and *Vauquelinia* (164). Perforations usually exclusively simple, a few scattered foraminate or reticulate plates occur in some species of *Amelanchier*, *Crataegus*, *Padus*, *Pourthiaea*, *Pyrus*, *Sorbaria*, *Sorbus*, and *Spiraea*, and according to Thompson (2254) in species of *Cydonia* and *Potentilla*. Intervascular pitting typically alternate, never large, minute in *Chaenomeles*, *Eriobotrya bengalensis* Hook. f., *Kageneckia*, *Laurocerasus*, *Malus*, *Photinia*, *Potentilla*, *Pygeum*, *Raphiolepis*, *Sorbaria*, and *Spiraea*; Tippo (2261) describes the pitting as mostly alternate and opposite and occasionally opposite or transitional; pits to ray cells similar to intervacular pits. The sieve-like

¹ Recorded by Solereder.

² Recorded by Solereder, but not observed in *Cydonia oblonga* Mill.

structures in *Prunus* and *Cerasus* referred to by Jönsson (1192) according to Bailey (78) are probably artefacts and not vested pits. Tyloses rare; deposits of gum present in some species, particularly in the Prunoideae. Mean member length of mature material about 0.4–0.95 mm.; Tippon, apparently including small stems, gives the range as 0.19–0.76 mm., with a mean of 0.487 mm. **Parenchyma** usually apotracheal only, in scattered cells or short uniseriate lines from ray to ray (Fig. 120 K) (short irregular metatracheal bands in *Pourthiaea*); very sparse, with occasional scanty paratracheal and diffuse cells (Fig. 120 J) in some species of *Kerria*, *Laurocerasus*, *Padus*, *Prunus*, *Rubus*, and *Spiraea*. Kanehira (1206) notes some paratracheal parenchyma in *Prinsepia*. Crystals in chambered cells or idioblasts in some species of *Cercocarpus*, *Chaenomeles*, *Crataegus*, *Eriolobus*, *Malus*, *Pseudocydonia*, and *Raphiolepis*. Solereder records the presence of silica in *Parastemon urophyllus* DC. Strands typically of 4 cells, occasionally up to 5 or 6. **Rays** multiseriate, mostly 2–5 cells wide, up to 6–10 cells wide in some species of *Hagenia*, *Padus*, *Prunus*, and *Spiraea*, more than 10 cells wide in some species of *Kerria*, *Rubus*, and *Spiraea*; over 1 mm. in height in *Hagenia*, *Kerria*, *Rubus*, and *Spiraea*; sometimes of 2 distinct widths. Uniseriates rather few and composed entirely of procumbent cells in woods with homogeneous rays; moderately numerous and composed of both procumbent and upright cells in most of the other genera, but composed only of square to upright cells in *Cotoneaster*, *Hagenia*, *Laurocerasus*, *Padus*, *Prinsepia* (1206), and *Stranvaesia*; uniseriates absent from *Kerria*. Typically 9–15 rays per mm., but only 3–5 per mm. in *Kerria*, *Rosa*, and *Rubus*. Homogeneous (Kribs's Type I) in *Cercocarpus*, *Crataegus*, *Cydonia*, *Malus*, *Micromeles*, *Padus*, *Polylepis*, *Pseudocydonia*, *Pyrus*, and *Sorbus*; heterogeneous (Kribs's Type II B), with 1 or 2 marginal rows of square or upright cells in most of the other genera, but more markedly heterogeneous (Kribs's Type II A) in *Cotoneaster*, *Hagenia*, *Laurocerasus*, *Prinsepia* (1206), and *Stranvaesia*; composed entirely of square to upright cells in some of the shrubby members, e.g. *Kerria*, *Rosa*, and *Rubus*; sheath cells occasionally present, e.g. in *Hagenia* and *Kerria*. **Fibres** with numerous distinctly bordered pits, equally numerous on both tangential and radial walls, except in the Pomoideae and some species of *Spiraea*, in which they are less numerous on the tangential walls.¹ Very fine septa and gum plates occur in occasional fibres in genera of the Prunoideae, and in *Spiraea alpina* Pall. and *Photinia lindleyana* Wight et Arn. Walls thin to thick, often radially flattened and with thicker walls towards the end of the growth ring; spiral thickening observed or reported in some species of *Amelanchier*, *Cercocarpus*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Heteromeles*, *Lyonothamnus*, *Mespilus*, *Osteomeles*, *Rosa*, *Stephanandra*. Mean length 0.9–1.6 mm. **Inter-cellular canals**. Traumatic vertical canals observed in one specimen of *Laurocerasus mackii* (Rupr.) C. K. Schum. and reported (1801, 1886) in some species of *Prunus* and *Pygeum*; radial canals reported (1801) in some specimens of *Pygeum*. **Growth rings**. The seasonal development of the rings in *Prunus*, *Pyrus*, and *Rosa* has been investigated by Coster (481).

¹ Solereder (2158) records occasional fibres with simple pits in *Kerria*, *Potentilla*, *Rhodotypos*, and *Spiraea*; Janssonius (1154) comments on the unusual difference between species of the same genus with respect to fibre pitting. Such a difference, for example, occurs between *Spiraea alpina* Pall. and *S. salicifolia* L., the borders being barely discernible in the latter.

ROOT

Roots of *Rosa* var. 'American Pillar' exhibit the following characters. Cork composed of thin-walled cubical cells with amorphous contents. Phloem strands, in transverse sections, shaped like tall triangles with outwardly directed apices; tending to be stratified into fibrous and unligified portions. Xylem exhibiting growth rings; vessels somewhat irregularly distributed, mostly solitary, very variable in diameter but seldom exceeding $100\ \mu$ in the material examined; primary rays up to about 8 cells wide in one specimen, but 20 or more cells wide in others, amyloiferous. Root structure similar in another, undetermined variety of climbing rose, but provided with a higher proportion of vessels of large diameter and less distinctly triangular phloem strands.

Wedge-like thickenings of the radial and transverse walls of the cells immediately external to the endodermis recorded in numerous genera by Solereder, and further examined, especially in *Gillenia*, by Holm (1928). The existence of a correlation between the anatomical structure of apple rootstocks and the vigour of the scions grafted on them has been established by Beakbane *et al.* (156-61). 'Vigour' in the scion is correlated with the relative proportions of different tissue elements revealed in transverse sections through rootstocks, the clearest connexion being with the proportion of wood ray tissue which is present. Living and dead tissues in the wood were found to be present in equal amounts in vigorous rootstocks, whereas in dwarfing stocks the proportion of living was two or three times greater than that of dead tissue. The vessels and xylem fibres were more numerous in the vigorous than in the dwarfing stocks, and the size of the vessels, although not definitely proportional to the vigour of the scion, tended to be larger in the vigorous stocks. Further results are to be expected from a continuation of these researches. See also under 'Economic Uses'. Differences in structure, of physiological rather than taxonomic interest, between 'large adventitious' and 'fibrous branch roots' recorded by White (2420) in the cultivated strawberry (*Fragaria*). The **developmental anatomy** of the root of the pear (*Pyrus communis* Linn.) has been described by Esau (659).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The considerable range of petiole structure within the family is interesting, the centric and hemicentric vascular strands in *Alchemilla*, *Eriobotrya*, and *Sanguisorba* being especially noteworthy. Those of *Alchemilla* in particular resemble some of those which occur in certain members of the Saxifragaceae, but it would be unwise, without taking exomorphic and other anatomical characters into consideration as well, to decide whether this provides evidence of affinity or represents a parallel development. The range of petiole structure in *Spiraea* (*sensu lato*) suggests that some members of this genus must be somewhat remotely related to others. The rather scanty information available suggests that *Laurocerasus* and *Prunus* should be regarded as distinct genera.

(ii) FROM WOOD STRUCTURE

The Prunoideae is the only tribe that can be distinguished from the others. It is characterized by (1) fibres with less distinctly bordered pits, which are

less numerous on the tangential than on the radial walls, and frequent plates of gum or fine septa, and (2) vessels that are commonly arranged in an oblique or radial pattern on the cross-section and often in multiples. The group is sometimes combined with the Chrysobalanoideae to form a separate family, the Amygdalaceae; Record and Hess (1886), however, point out that 'from the standpoint of the woods the Prunoideae belong with the Rosaceae and the Chrysobalanoideae seem distinct enough to be segregated into a family of their own'.

In the Pomoideae and also in *Cercocarpus* and *Adenostoma* of the Rosoideae and *Quillaja* of the Spiraeoideae the vessels are almost exclusively solitary. In the latter two tribes the vessels in the other genera are often grouped tangentially or in clusters.

Spiral thickening of the vessels and distribution of parenchyma have been suggested by Janssonius (1154) as a means of distinguishing between the tribes, but have not proved to be valid characters for the larger number of genera and species here investigated.

Lyonothamnus. This genus, mentioned by Dalla Torre et Harms under Rosaceae as a genus of uncertain position, is referred by Britton and Shafer, *North American Trees*, p. 408 (1908), to the family Cunoniaceae. Its wood anatomy is quite consistent with its being a member of the Rosaceae, though not of the tribe Prunoideae. It does not fit so well in the Cunoniaceae.

Prunus and *Laurocerasus*. Though it is not possible to separate all the specimens of these 2 genera into 2 sharply defined groups there does appear to be an appreciable divergence. *Laurocerasus* tends to have very definitely heterogeneous rays, frequently with 4 or more marginal rows of upright cells, and some vasicentric parenchyma, and some species (*L. officinalis* Roem., *L. lusitanica* Roem., and *L. lyoni* Britton) have a marked radial vessel pattern. In *Prunus* the rays are more homogeneous, the marginal rows seldom being more than 1-3 and their cells square rather than upright, the parenchyma is diffuse only and often very sparse; some species have an oblique vessel pattern, but this is less definite and more nearly tangential than in the extreme forms of *Laurocerasus*. Examples of the tendency for the 2 groups to overlap are provided by the following species: *Laurocerasus maackii* (Rupr.) C. K. Schn., which has the structure typical of a *Prunus*, and *Prunus annularis* Koehne, which might be a typical *Laurocerasus*.

ECONOMIC USES

Many species are cultivated as ornamental shrubs, whilst other members of the family yield edible fruits such as the Loquat (*Eriobotrya japonica* Lindl.), Strawberry (*Fragaria vesca* Linn.), Bitter Almonds (*Prunus amygdalus* Batsch. var. *amara* Schneid.), Sweet Almonds (*Prunus amygdalus* Batsch. var. *dulcis* Schneid.), Apricot (*Prunus armeniaca* Linn.), Plum (*Prunus domestica* Linn.), Peach (*Prunus persica* Batsch), Pear (*Pyrus communis* Linn.), Apple (*Malus pumila* Mill.), and Blackberry and Raspberry (*Rubus* spp.). Other economic products include *Quillaja* bark (*Quillaja saponaria* Mol.), which is used as a commercial source of saponin and for medicinal purposes. This bark can be recognized by a narrow layer of cork cells with red-brown contents; tortuous bundles of phloem fibres; abundant starch grains, usually 5-10 but sometimes up to 20 μ in diameter; calcium oxalate crystals 170 μ long and 30 μ wide.

The existence of several types of *Quillaja* bark, exhibiting variations in structure, has been reported, but these are probably from branches of different age or from plants grown in various habitats. For further particulars see papers by Holmes (1075, 1076) and Cofman-Nicoresti and Tallantyre (440).

Beakbane and Thompson (159) have shown that the 'rubbery' condition of certain parts of the wood of 'Lord Lambourne' and other cultivated varieties of apple-trees is due to lack of lignification of the wood fibres. In consequence the affected stems and branches are abnormally flexible. In other cases unusually flexible stems of apple and pear varieties and of some apple root-stocks were found to be due to an abnormally large pith, or to a high proportion of living cells in the wood. When the 'rubbery' condition is due to imperfect lignification, this can be immediately demonstrated by treatment with phloroglucinol and hydrochloric acid. The cause of the disease is at present uncertain. (See also under 'Root'.)

Other recent work on the anatomy of rosaceous fruit-trees includes the investigation by MacDaniels and Cowart (1407) concerning the structure and development of the apple leaf, and that by Schneider (2046) dealing with the structure of the phloem in peach and cherry.

The anatomy of species of *Dryas*, *Geum*, and *Sieversia* which are used in folk medicine has recently been described by Schulthess (2048).

The woods of this family are not of great importance. The best-known timbers are probably various cherries (*Prunus* spp.), particularly the American Black Cherry, *P. serotina* Ehr., and the European Cherry, *P. avium* L., which provide ornamental timbers. The wood of the Pear, *Pyrus communis* L., has some special uses, e.g. as a substitute for boxwood for engraving.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acaena, Agrimonia,* Alchemilla,* Amelanchier,* Chaenomeles, Coton-easter,* Cliffortia, Crataegomespilus,* Crataegus,* Cydonia,* Dichotomanthes,* Eriobotrya,* Filipendula, Fragaria,* Geum,* Gillenia,* Heteromeles, Kagineckia, Kerria,* Laurocerasus,* Lindleya, Mespilus, Neillia,* Neurada, Neviusa,* Osteomeles, Photinia,* Potentilla,* Poterium,* Prinsepia, Prunus,* Pygeum, Pyracantha,* Pyrus,* Quillaja,* Raphiolepis,* Rosa,* Rubus,* Sanguisorba, Sibiraea, Sorbus,* Spiraea,* Stranvaesia,* Vauquelinia, Waldsteinia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Adenostoma, Amelanchier, Cercocarpus, Chamaebatia, (Cliffortia), Coton-easter, Crataegus, Cydonia, Eriobotrya, Eriolobus, Exochorda, Fallugia, Hagenia, Heteromeles, Holodiscus, Kagineckia, Kerria, Laurocerasus, Lyonothamnus, Malus, Mespilus, Micromeles, Nuttallia, Osteomeles, Padus, Photinia, Physocarpus, Polylepis, Potentilla, Pourthiaea, Prunus, Pseudocydonia, Purshia, Pygeum, Pyrus, Quillaja, Raphiolepis, Rosa, Rubus, Sorbaria, Sorbus, Spiraea, (Vauquelinia).

LITERATURE

(i) *On General Anatomy* (including Chrysobalanoideae)

Aubertot 48, Batrany 152, Beakbane *et al.* 156, 157, 158, 159, 160, 161, Betts 187, 188, 189, 190, Bird 199, Bowman 250, Brierley 269, Brooks 278, Butler 324, Carlson 342, Cofman-Nicoresti and Tallantyre 440, Dorsey and Weiss 607, Esau 659, Foweraker 703, Gleichgewicht 789, Gregory 815, Greguss 2522, Gyhr 854, Haberlandt 858, 859, 860, 861, Holm 1028, 1039, 1045, Holmes 1075, 1076, Knapheisowna 1249, Lepeschkin 1361, Löw 1397, MacDaniels and Cowart 1407, McCown 1464, Montcheff 1553, Morvillez 1556, 1557, Price 1741, Priestley and Hinchliff 1751, Prodinger 1760, Rinde 1939, Sabnis 1977, Schneider 2046, Schulthess 2048, Starr 2188, Watkins 2367, Weiss 2391, White 2420, Woodcock 2460, Youngken 2496.

(ii) *On Wood Structure* (including Chrysobalanoideae)

Bausch 154, Beakbane *et al.* 156, 157, 161, Beekman 167, Benoist 170, den Berger 179, 182, den Berger and Endert 183, Besson 186, Bianchi 194, Bienfait and Pfeiffer 197, B. H. For. Dept. 274, Brown and Panshin 288, 289, Burgerstein 310, 312, Chalk and Rendle 365, Coster 481, Cozzo 494, Dadswell and Record 533, Descole and O'Donnell 576, Foxworthy 705, Gonggrijp 794, Hale 870, Howard 1088, van Iterson 1126, Janssonius 1154, Jones 1191, Jönsson 1192, Kanehira 1206, 1209, Lecomte 1334, Macduffie 1408, Malhorta 1430, Martin-Levigne 1450, Nicoloff 1593, Pearson and Brown 1679, Pfeiffer, J. Ph. 1713, Record 1780, 1781, 1783, 1787, 1800, 1801, 1818, 1843, 1851, Record and Hess 1886, Stone 2202, 2203, Tang 2230, 2231, Thompson 2254, Tippe 2261, Torres 2269, Uspensky 2317, Williams 2430, Yamabayashi 2478, Yatsenko Khmelevsky and Djaparidze 2488.

117 A. ROSACEAE (CHRYSOBALANOIDEAE)

(FIG. 121 on p. 552)

SUMMARY

(i) GENERAL

A tropical, chiefly American family, consisting of trees and shrubs. The **stomata** are rubiaceous. Transverse sections through the distal end of the **petiole** generally exhibit a closed ring of xylem and phloem accompanied by two small adaxial vascular strands, but numerous modifications of the closed ring are to be found in different genera or even in different species of a single genus. The **cork** generally arises superficially. The **pericycle** exhibits a ring of sclerenchyma which is usually continuous, but may be broken. Stone cells, which occur in the pericycle, are generally characterized by being thickened only on one side, thus appearing U-shaped in transverse section. Silicified cell membranes and solid inclusions of **silica** are common.

(ii) WOOD

Vessels moderately to very large, almost exclusively solitary, few to moderately numerous, typically in oblique lines, spiral thickening absent, perforations exclusively simple, pits to ray cells always including some that are larger than the intervacular pitting; members of medium length. **Parenchyma** apotracheal, predominantly in uni- to triseriate bands. **Rays** exclusively or predominantly uniseriate; heterogeneous. **Fibres** with numerous distinctly bordered pits; of medium length.

LEAF

Whole **mesophyll** usually consisting of palisade tissue except in *Lecostemon*. Long, unicellular, arachnoid **hairs** with thin walls form a web-like covering to the leaves of *Couepia*, *Licania*, *Moquilea*, *Parinari*; stellate hairs occur in

Chrysobalanus, and peltate ones in *Lecostemon*. **Glands** present at the leaf base of certain species of *Parinari*, and especially large and conspicuous ones in *Acioa*, *Chrysobalanus*, *Couepia* (pro parte), *Hirtella*, *Licania*, *Moquilea*. **Cork warts** recorded on the leaf of *Couepia bracteosa* Benth. **Epidermis** composed of cells with mucilaginous walls in species of *Chrysobalanus*, *Grangeria*, *Hirtella*, *Parinari*; papillose on the lower surface in *Couepia*. Epidermal cells frequently palisade-like. **Hypoderm** present in *Chrysobalanus*, *Couepia*, *Grangeria*, *Hirtella*, *Lecostemon*, *Licania*, *Moquilea*, *Parastemon*, *Parinari*. **Stomata** recorded only on the lower surface except in *Stylobasium*; rubiaceous. **Mesophyll** traversed by fibre-like 'spicular cells' in *Couepia*, *Lecostemon*, and *Licania*. Vascular bundles of the **veins** (except in *Stylobasium*) surrounded by sclerenchymatous fibres, which exhibit U-shaped thickenings in transverse sections; vertically transcurrent in certain species of *Acioa*, *Chrysobalanus*, *Couepia*, *Hirtella*, and *Licania*. Terminal tracheids with wide lumina in *Licania* and *Moquilea*. Transverse sections through the distal end of the **petiole** described by Morvillez (1557) as exhibiting an abaxial closed ring of xylem and phloem which shows various modifications towards the adaxial side in different genera and species. The ventral strand, in all recorded instances, accompanied by 2 small separate adaxial bundles. Modifications are as follows. (i) The main ring of xylem and phloem somewhat invaginated on the adaxial side in *Hirtella*. (ii) As (i) but with the invagination expanded laterally at the base in *Parinari*. (iii) Main vascular strand in *Licania* enclosing a solid medullary bundle with central xylem surrounded by phloem. (iv) Similar to (iii) but with the xylem of the medullary strand confined to the adaxial surface of the phloem in *Moquilea guianensis* Aubl. (v) Main vascular strand consisting of 2 closed concentric rings of xylem and phloem surrounding 2 small, solid bundles in *Moquilea sclerophylla* Mart. (vi) Main vascular strand enclosing 1 large and several small solid strands in *Moquilea licaniflora* Sagot. (vii) Main vascular strand enclosing a greatly reduced central bundle consisting of an island of phloem in *Chrysobalanus icaco* Linn. Transitional stages between these types also occur. **Silicified membranes** common except in *Lecostemon* and *Stylobasium*; silica bodies recorded in the epidermal cells and in the neighbourhood of the leaf veins of all examined genera except *Parastemon* and *Stylobasium*. Similar bodies also occur in the peltate hairs of *Lecostemon*; in the mesophyll of the leaf of some species of *Couepia*, *Lecostemon*, and *Moquilea*. Silica deposits in certain species of *Chrysobalanus* and *Hirtella* sometimes enclose clustered **crystals**. **Secretory cavities** recorded in *Couepia bracteosa* Benth. and in *Lecostemon* spp.

AXIS

YOUNG STEM

Cork, generally superficial in origin. **Pericycle** including strands of primary fibres which subsequently become united by stone cells, the latter showing horseshoe-shaped thickenings in transverse sections. **Xylem** in the form of a continuous cylinder traversed by narrow rays. Vessels with simple perforations. **Idioblasts** containing **tannin** present in the phloem of certain species of *Couepia*, *Moquilea*, and *Parinari*. **Silica bodies** stated to occur in the pericycle, medullary rays, and pith of all the genera examined except

Parastemon and *Stylobasium*. Similar bodies also recorded in the bark of *Hirtella americana* Linn.

WOOD (Fig. 121)

Vessels mostly moderately large (mean tangential diameter 200–300 μ m.), very large in *Chrysobalanus* and *Parinari*; exclusively solitary or nearly so; typically in oblique lines; few in most species (less than 5 per sq. mm.); moderately numerous (5–20) in *Licania* and *Chrysobalanus*; spiral thickening absent; perforations exclusively simple; intervacular pitting alternate, never

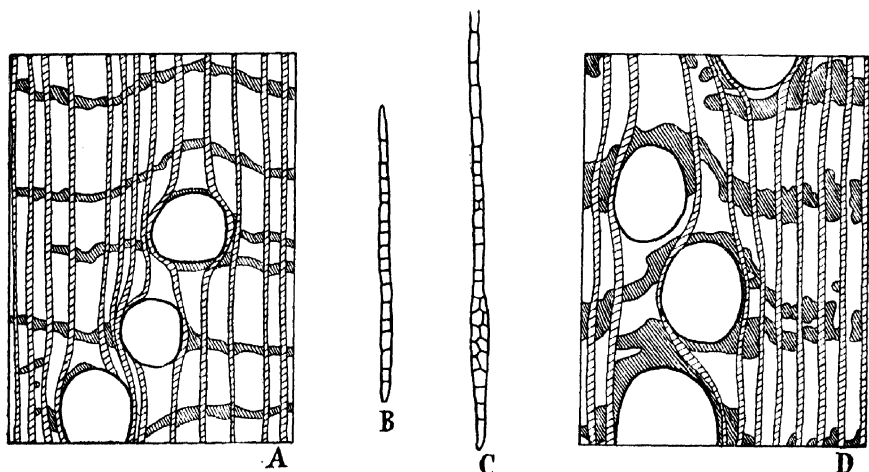


FIG. 121. ROSACEAE—CHRYSOBALANOIDEAE

A, *Licania heteromorpha* Benth. B, *L. hypoleuca* Benth. C, *Parinari asperulum* Miq.
D, *P. mobola* Oliv.

minute; some of the pits to ray cells and parenchyma always larger than the intervacular pits and oblong; tyloses sometimes present, sclerosed in *Angelesia*. Mean member length 0.6–0.8 mm. **Parenchyma** apotracheal only, in numerous fine continuous bands, usually 1 (locally 2) cells wide and 6–11 per mm.; 2–3 cells wide and usually slightly less numerous (less than 6 per mm.) in *Acioa* and the African species of *Parinari*, strands typically of up to 16 cells. **Rays** fine, exclusively uniseriate in *Chrysobalanus*, *Couepia*, *Grangeria*, *Hirtella*, and *Licania*, and predominantly uniseriate, but with some biseriate rays in the others; more than 1 mm. high in *Acioa*, *Couepia*, *Licania*, *Parastemon*, and some species of *Parinari*; 12–20 per mm.; heterogeneous Kribs's Type III; almost homogeneous in *Parastemon*. Silica is reported in the ray cells of *Angelesia splendens* Korth., *Parastemon inophyllum* A. DC. (794) and *Parinari* spp., and van Iterson (1126) states that the Chrysobalanoideae is very rich in silica inclusions. **Fibres** with numerous distinctly bordered pits on the tangential walls, more numerous and often biseriate in the wider cells bordering the vessels; pits on the radial walls almost entirely limited to areas in contact with rays; walls thick (except in *Couepia* and some species of *Licania*). Mean length 1.3–1.4 mm.

TAXONOMIC NOTES

FROM WOOD STRUCTURE

The genera of this group are very uniform in structure and form a distinct group that is easily separated from the rest of the Rosaceae; the most characteristic features are the banded apotracheal parenchyma, the oblique pattern of the vessels, the almost exclusively uniseriate rays, and the long parenchyma strands of up to 16 cells.

There is no very distinct evidence of this group being at a different level of specialization from the rest of the Rosaceae. As Tippo (2261) has pointed out, both are more specialized than the Cunoniaceae.

ECONOMIC USES

The Coco Plum is derived from *Chrysobalanus icaco* Linn. The bark of the Caraipi tree of Para (*Moquilea utilis* Hook. f.) is mixed with clay to make vessels for domestic use. The timbers are very similar throughout the group. They are not widely used.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acioa, Chrysobalanus, Couepia, Grangeria, Hirtella, Lecostemon, Licania, Moquilea, Parastemon, Parinari, Stylobasium.

(ii) FOR WOOD STRUCTURE

Acioa, Angelesia, Chrysobalanus, Couepia, Grangeria, Hirtella, Licania, Parastemon, Parinari.

LITERATURE, *see* Rosaceae, p. 550

118. SAXIFRAGACEAE

(FIG. 122 on p. 556)

SUMMARY

Herbs, sometimes tending to be succulent. The family occurs particularly in temperate and cold regions. The **leaf** is dorsiventral or centric. Both glandular and non-glandular types of **hair** are common. The leaf **epidermis** sometimes includes a proportion of elongated cells with tanniniferous contents. The **stomata** are usually ranunculaceous, but their distribution may be of considerable specific diagnostic value. **Hydathodes** are common, and in some instances secrete water containing calcium bicarbonate which becomes deposited on the leaf surface as solid carbonate. Hydathodes which secrete lime in this way are known as **chalk glands**. **Crystals** are rare, but clustered where present. The occurrence in the **petiole** of one or more separate bundles, each surrounded by an endodermis, is an interesting feature of certain species of *Saxifraga*, and somewhat recalls the petiolar structure in *Alchemilla* (Family Rosaceae). The stem exhibits a **vascular system** composed of individually distinct bundles in some species; in others the primary rays are narrower and the xylem continuous. There is frequently a continuous

ring of fibres in the **pericycle**. **Cortical** and/or **medullary bundles** have been recorded. The nodes of *Parnassia palustris* Linn. are said to be polystelic.

LEAF

Dorsiventral in *Astilbe*, *Chrysosplenium*, *Heuchera*, *Hoteia*, *Mitella*, *Saxifraga* (pro parte), *Tellima*, *Tiarella*, *Zahlbrucknera*; isobilateral or centric in *Saxifraga* (pro parte, especially the section *Porphyrium*), and *Vahlia*. **Hairs** glandular and non-glandular.

I. *Non-glandular*. (i) Simple, uniseriate; common in *Saxifraga*. (ii) Shaggy in *Saxifraga*. (iii) Multicellular, multiseriate recorded in *Astilbe*, *Boykinia*, *Heuchera*, *Peltiphyllum*, *Tiarella*, *Tolmiea*. (iv) Fimbriate appendages, secreting mucilage when young, in *Parnassia*.

II. *Glandular*. (i) Uniseriate with a unicellular or multicellular head in *Boykinia*, *Francoa*, *Heuchera*, *Peltiphyllum*, *Saxifraga*, *Suksdorfia*, *Tetilla*, *Tiarella*, *Tolmiea*, *Vahlia*, *Zahlbrucknera*. (ii) Glandular shaggy, with a multicellular stalk and head in *Astilbe*, *Hoteia*, *Mitella*, *Saxifraga*, *Tellima*, *Tiarella*.

Epidermis composed of cells with straight or sinuous anticlinal walls. Long vermiform cells with tanniniferous contents occur between and sometimes project above the ordinary epidermal cells in species of *Chrysosplenium*, *Lepuropetalon*, *Parnassia*, *Saxifraga* (section *Cymbalaria*), *Zahlbrucknera*; frequently recognizable in herbarium material as small brown striae. **Stomata** present on one or both surfaces; ranunculaceous, e.g. in the *Dactyloides*, *Nephrophyllum*, and *Miscopetalum* sections of *Saxifraga*; subsidiary cells sometimes smaller than their neighbours, e.g. in *Saxifraga*, section *Euaizoonia*. The distribution of stomata is probably of considerable specific diagnostic value in *Chrysosplenium* and *Saxifraga*. Stomata confined to the upper surface in some species of *Saxifraga*; occurring on both surfaces at the tips of the leaves in others; restricted to the leaf margins in a third group; confined to the middle on the upper and to the margins on the lower surface in a fourth group. Stomata in *Chrysosplenium* restricted to the lower side in the *Alternifolia* group, but occurring on both surfaces in the section *Dialysplenium*; occasionally in groups in both sub-genera. Hryniewicz (1900) records the existence of guard cells with a distinctive type of structure in various members of the family, but the utility of this character for diagnostic purposes is limited by the difficulty of rapidly cutting sections of sufficiently good quality to show what is required. **Hydathodes** recorded in *Chrysosplenium*, *Heuchera*, *Mitella*, *Saxifraga*, *Tellima*, *Zahlbrucknera*, and probably occurring in other genera as well, although apparently absent from *Bergenia*; those in *Saxifraga* mostly situated at the leaf margins, at the tip of the leaf, or at the bases of the leaf teeth, sometimes in depressions (e.g. in the sections *Euaizoonia*, *Kabschia*, *Porphyrium*, *Xanthizoon*), more rarely on the leaf surface; always above the terminations of veins. Hydathodes sometimes secrete lime in the form of a solution of calcium bicarbonate, from which solid **calcareous deposits** are formed on the surface of the plant. Hydathodes which secrete calcareous material in this way are known as chalk glands. The quantity of lime secreted is governed by the nature of the soil. Further details concerning hydathodes and chalk glands have been recorded by Kurt (1908). **Mesophyll** not pos-

sessing great diagnostic value owing to its variability in different species and also in relation to the environment; not differentiated into palisade and spongy portions in certain species of *Saxifraga*. Number of palisade layers, where differentiated, ranging from 1 to 7. **Petiole.** Structure, in transverse section, somewhat distinctive, especially in *Saxifraga*, owing to the presence of at least one concentric or hemi-concentric bundle. Many species of *Saxifraga* (Fig. 122 K) are provided with 3 such bundles each surrounded by a separate endodermis, and in this respect resemble *Alchemilla* (Fig. 119 C) (Family Rosaceae). Three separate bundles also observed in species of *Heuchera* (Fig. 122 I) but in this genus they are collateral. The thick, fleshy petiole of *Bergenia delavayi* (Franch.) Engl. (Fig. 122 M) is supplied by numerous, irregularly scattered bundles. For further details concerning the vascular structure of the petiole see Morvillez (1559). **Secretory cells** with unidentified but probably tanniniferous contents seen to be common in the unligified tissues of the petiole and recorded in species of *Chrysosplenium*, *Lepuropetalon*, *Parnassia* (Thompson 2252), *Saxifraga* (*Cymbalaria*), and *Zahlbrucknera*. Clustered **crystals** observed or recorded in a few species; rare in *Saxifraga*.

AXIS

STEM (Fig. 122 N)

Cork usually arising in the outermost layer of the pericycle; but originating in the sub-epidermis in *Peltiphyllum* and in the epidermis itself in *Vahlia*. **Cortex** sometimes very lacunar, e.g. in *Bergenia delavayi* (Franch.) Engl. **Pericycle** containing a broad continuous ring of fibres in the few species of *Heuchera* and *Saxifraga* examined; fibres confined to separate strands at the outer periphery of the phloem in *Bergenia delavayi*. According to Engler (636) sclerenchyma is absent from the flowering stem of the *Cymbalaria* section of *Saxifraga* and from certain species in other sections of the genus as well. **Phloem** and **xylem** usually appearing in transverse sections as individually distinct collateral bundles (Fig. 122 N), but the primary rays between them are sometimes rather narrow. There are considerable variations in this respect even within the genus *Saxifraga*. For further details see Engler (636). Vessels usually small; radial diameter not exceeding $15\ \mu$ in *Bergenia delavayi*; up to about $30\ \mu$ in *Heuchera* spp. Only simple perforations observed. **Pith** observed to be very lacunar in species of *Bergenia*, *Heuchera*, and *Saxifraga*. **Medullary bundles** recorded in a considerable number of species of *Saxifraga*, particularly but not exclusively in the section *Euaizoonia* as well as in *Peltiphyllum* and *Rodgersia*. **Cortical bundles** also reported in *Peltiphyllum*. Stems polystelic at the nodes in *Parnassia palustris* Linn. **Secretory cells** with tanniniferous contents recorded in the unligified tissues in species of *Chrysosplenium*, *Lepuropetalon*, *Parnassia*, *Saxifraga*, *Zahlbrucknera*, and also observed in *Heuchera*.

TAXONOMIC NOTES

The Saxifragaceae in the Bentham and Hooker system included plants which have been described in this book under Cunoniaceae, Grossulariaceae, Escalloniaceae, and Hydrangeaceae. Engler likewise (636) included all of these groups under Saxifragaceae, but he recognized the existence of a number

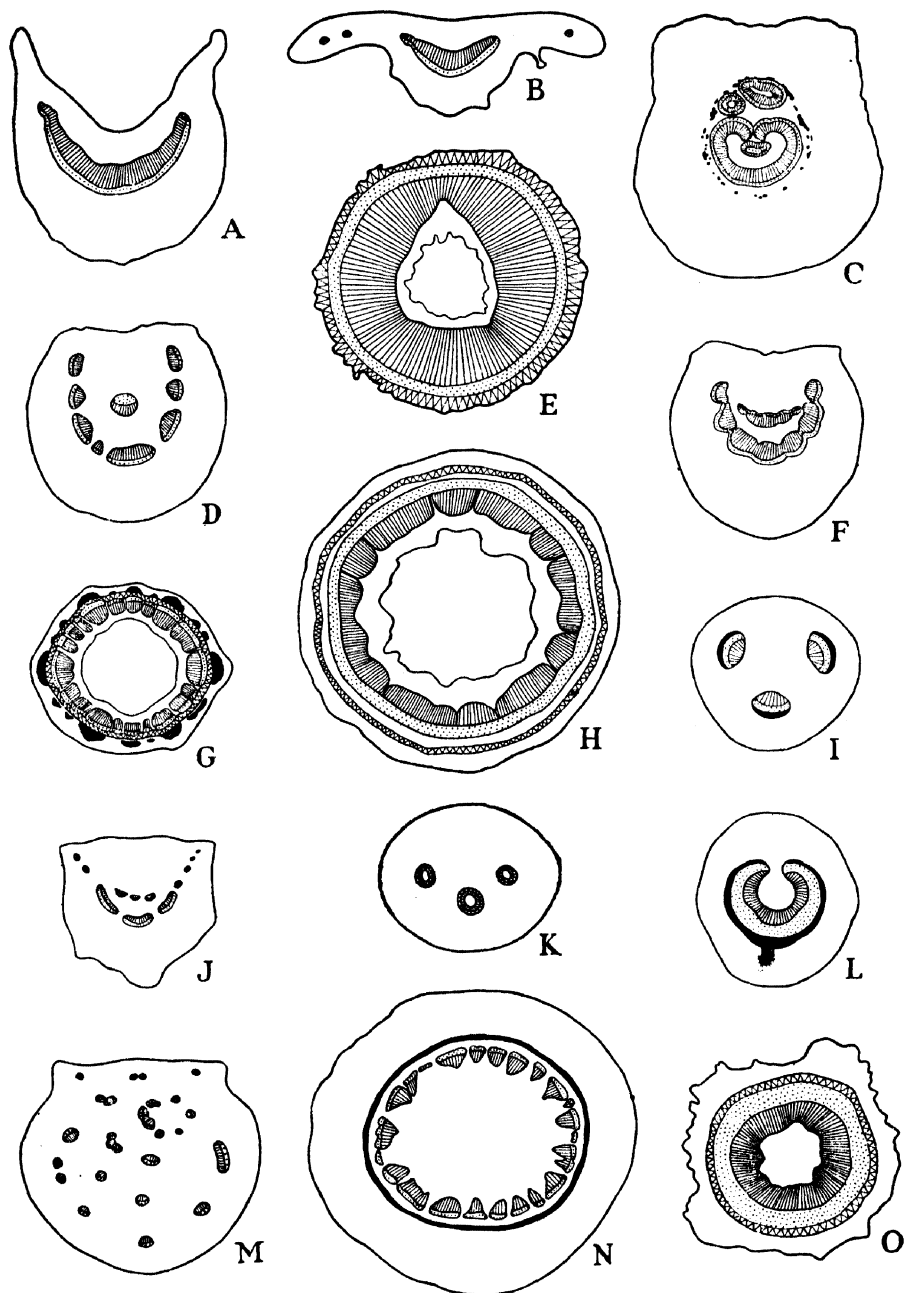


FIG. 122. *HYDRANGEACEAE*, A, D, F-H, J; *ESCALLONIACEAE*, B-C and E; *SAXIFRAGACEAE*, I, K, and M-N; *GROSSULARIACEAE*, L and O

A, *Deutzia setchuensis* Franch. Petiole $\times 13$. B, *Escallonia rubra* Pers. Petiole $\times 12$. C, *Brexia madagascariensis* Thou. Petiole $\times 12$. D, *Hydrangea arborescens* Linn. Petiole $\times 13$. E, *Escallonia macrantha* Hook. et Arn. Stem $\times 13$. F, *Hydrangea petiolaris* S. et Z. Petiole $\times 13$. G, *Philadelphus pubescens* Lois. Stem $\times 15$. H, *Hydrangea arborescens* Linn. Stem $\times 13$. I, *Heuchera americana* Linn. Petiole $\times 7$. J, *Dichroa febrifuga* Lour. Petiole $\times 7$. K, *Saxifraga fortunei* Hook. Petiole $\times 8$. L, *Ribes sanguineum* Pursh. Petiole $\times 18$. M, *Bergenia delavayi* Engl. Petiole $\times 5$. N, *Saxifraga fortunei* Hook. Stem $\times 13$. O, *Ribes grossularia* Linn. Stem $\times 18$.

of sub-families. Hutchinson treats the Saxifragaceae (*sensu stricto*) as if evolved along a different line from the Cunoniales in which he includes the other families mentioned above. It is thus clear that taxonomists are by no means agreed concerning the interrelations of the groups concerned. It will at once be appreciated that the Saxifragaceae, as treated in this book, constitute a wholly herbaceous family, whereas the other groups in question are composed of woody plants. For this reason alone one would expect to find anatomical distinctions between them, but in practice the differences are not of a kind which are usually to be found between herbs and woody plants which are closely related to one another. It has been questioned by Arber (see 2254) whether *Parnassia* truly belongs to the Saxifragaceae or has closer affinities with the Hypericaceae. It is sometimes treated as a member of a separate family, the Parnassiaceae.

ECONOMIC USES

Numerous members of the family are cultivated for ornamental purposes, especially in rock-gardens.

GENERA DESCRIBED

Astilbe, Bauera, Bergenia,* Boykinia, Chrysosplenium, Colmeiroa, Deinanthé, Francoa, Heuchera,* Hoteia, Lepuropetalon, Mitella, Parnassia, Peltiphyllum, Rodgersia, Saxifraga,* Suksdorfia, Tellima, Tetilla, Tiarella, Tolmiea, Vahlia, Zahlbrucknera.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Briquet 271, Engler 636, Engler and Irmscher 644, Hryniewiecki 1100, Kurt 1308, Morvillez 1559, Smith, H. 2150, Thompson, H. S. 2252.

119. CEPHALOTACEAE

(FIG. 123 on p. 558)

SUMMARY

Cephalotus follicularis Labill., the sole representative of the family, is a perennial herb with an underground rhizome, the lower of whose basal leaves are differentiated as pitchers similar to those of *Nepenthes*, the upper leaves of the basal rosette being ordinary photosynthetic organs. The plant is confined to marshes in King George's Sound, South-west Australia. The most interesting anatomical feature is the occurrence of glands in the pitchers which are thought by some authorities to secrete substances capable of digesting animal food. The morphology and anatomy of the plant has been recently surveyed by Lloyd (1383), whilst an earlier account by Macfarlane (1411) includes a very complete description of the anatomy of the whole plant. Another important description was published by Schweiger (2063). The particulars given below have been taken from these sources.

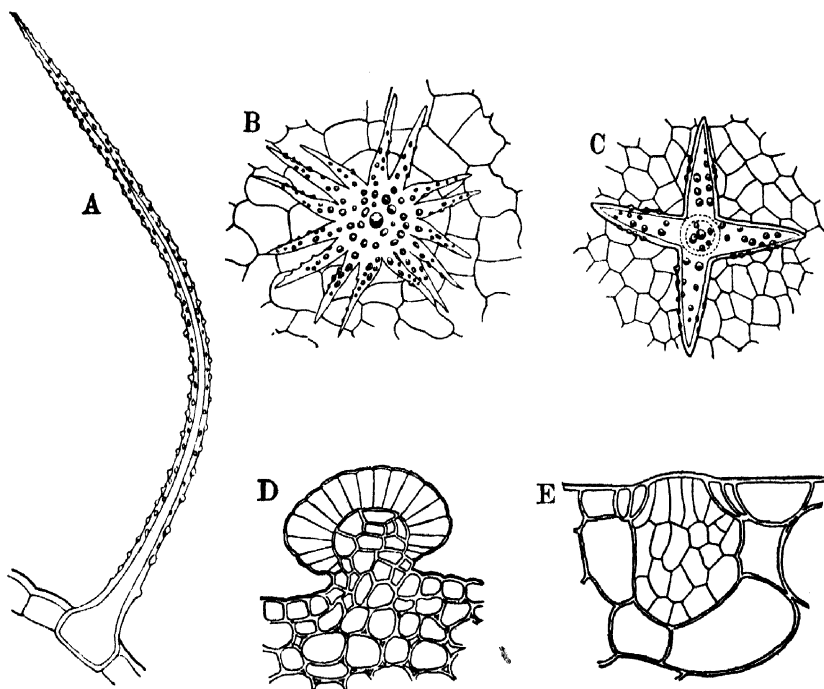


FIG. 123. *HYDRANGEACEAE*, A-C; *ESCALLONIACEAE*, D; *CEPHALOTACEAE*, E

A, Simple trichome of *X Philadelphus insignis* Carr. B, Stellate hair from the upper side of the leaf of *Deutzia pulchra* Vidal. C, Stellate hair from the upper side of the leaf of *Deutzia gracilis* Sieb. et Zucc. D, Stem-gland of *Escallonia viscosa* Forbes. E, Gland of *Cephalotus*—A-C, by Solereder; D, after Thouvenin; E, After Goebel.

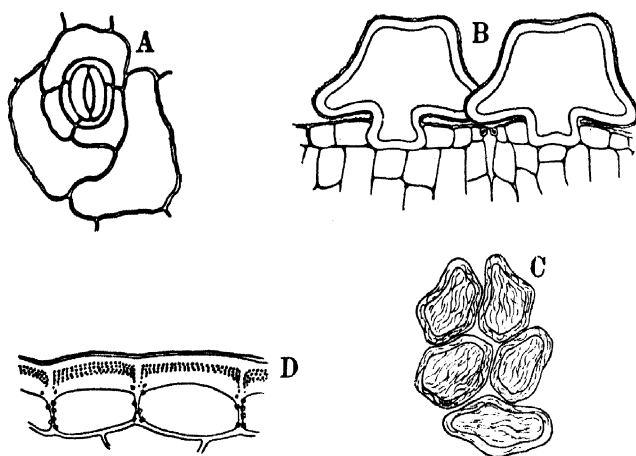


FIG. 124. *CRASSULACEAE*

A, Type of stoma in *Sedum spurium* Marsch. Bieb. B, C, Bladder-like epidermal cells of *Crassula falcata* Wendl. D, Transverse section through the epidermis of the anterior portion of the leaf of *Sempervivum calcareum* Jord.—A after Strasburger; B, C after Areschoug; D after Solms-Laubach.

LEAF

(a) SCALE LEAVES ON ELONGATED PARTS OF THE AXIS

Unicellular **hairs** present on both surfaces and along the margins; accompanied by **glands** similar to those on the foliage and pitcher leaves. **Mesophyll** poorly developed, traversed by a few, small vascular bundles.

(b) FOLIAGE LEAF

Unicellular **hairs** with solid tips and brownish contents towards the base, present on the petiole and at the margins of the lamina. **Glands** (Fig. 123 E) also occur on the petiole and lower surface of the lamina. **Stomata** situated on both surfaces, but most numerous on the lower side and also occurring on the petiole. **Mesophyll** approximately isobilateral, but palisade cells somewhat rounded and not quite equally developed towards both surfaces; central portion composed of very lacunar spongy tissue. According to Macfarlane (1411) the single bundle system which enters the base of the **petiole** 'splits into one median and two lateral parts. The median part consists of four bundles so placed that two of them are lateral, one inferior and one superior, but with their xylems inclined towards each other, and their extra-phloem sclerenchyma patches directed outwardly.'

(c) PITCHER LEAVES

Epidermis on the outside of the pitcher composed of isodiametric cells, perforated by **stomata** and bearing depressed glands and unicellular **hairs**. Inner surface of the lid consisting for the most part of a so-called 'slippery surface' composed of downwardly projecting, overlapping, striated projections from the epidermal cells. **Glands** (Fig. 123 E) similar to those on the external surface also present. Glands in the interior of the pitcher flask-shaped; those present on the brightly coloured, cushion-like projections, which extend into the interior of the pitcher, being especially large. **Hydathodes** also recorded on the projections. Glands said to be absent from the lower part of the internal wall of the pitcher. Full details concerning the vascular system of the pitcher are given in the special articles mentioned above, but it is interesting to note that Lloyd says: 'The venation is derived from two systems of bundles in the petiole, a dorsal of three veins, and a ventral of two, these splitting near the pitcher into four, then six and branching further in spreading.'

AXIS

RHIZOME

Epidermis in the young rhizome bearing long, unicellular hairs. **Cork** formation is initiated during the first year. **Cortex** fairly broad; amyliiferous according to Macfarlane (1411) and tanniniferous according to Schweiger (2063). **Vascular system** composed of a ring of phloem and xylem interrupted by broad, foliar traces. **Pith** similar to the cortex. Brown deposits present in the epidermis, cortex, and pith of old rhizomes.

ROOT

Epidermis pale coloured. **Cortex** composed of 2 or 3 layers of cells. **Endodermis** consisting of flattened cells. **Cork** arising in the pericambium,

consisting, in mature roots, of 3 or 4 layers of cells, but according to Macfarlane (1911) the endodermis and cortical tissues do not become detached. Schweiger (2063), on the other hand, describes an old root as covered externally by a layer of cork bounded on the inside by rounded, mostly tanniferous cells. **Stele** triarch. Xylem vessels described by Schweiger as having scalariform perforation plates, but this needs confirmation.

TAXONOMIC NOTES

The similarity of the pitchers of *Cephalotus* to those of *Sarracenia* and *Nepenthes* is probably due to parallel development. There are no close taxonomic affinities between these plants.

GENUS DESCRIBED

Cephalotus.

LITERATURE

On General Anatomy

Arber 32, Diels 584, Lloyd 1383, Macfarlane 1411, Schweiger 2063.

120. CUNONIACEAE

(FIG. 125 on p. 562; FIG. 126 on p. 570)

SUMMARY

(i) GENERAL

Trees and shrubs mainly from Australasia. Some of the more important anatomical characters include the occurrence of specially small **stomata** whose guard cells are almost circular in outline; in twigs, the **xylem** with uniseriate rays and small, often somewhat angular vessels, mostly with scalariform perforation plates; the heterogeneous **pith**; the common occurrence of **secretory cells** with tanniferous or mucilaginous contents.

(ii) WOOD

Vessels moderately small, solitary or with some multiples, perforation plates scalariform only or simple with a few scalariform plates, rarely simple only; intervacular pitting scalariform to opposite, rarely alternate; pits to parenchyma typically large and horizontally elongated; members moderately long. **Parenchyma** apotracheal, diffuse or in bands 1-4 cells wide. **Rays** up to 2-4 cells wide, markedly heterogeneous in most species. **Fibres** usually with distinctly bordered pits; of medium length.

LEAF

Dorsiventral in all of the species examined. **Hairs** sometimes absent, but chiefly represented by infrequent unicellular types. Tufted hairs recorded in *Callicoma*, and glandular shaggy ones in *Ceratopetalum* and *Cunonia*, the latter occurring particularly on the stipules and leaf teeth. Cells of the **epidermis** elongated and palisade-like in *Codia montana* Forst., *Cunonia* (locally), *Weinmannia trichosperma* Cav. **Stomata** particularly small and

almost circular in outline in *Cunonia* and *Platylophus*; guard cells of *Belangeria* with ridge-like humps which appear like small horns in a transverse section of a leaf. **Hypoderm**, frequently consisting of 3 layers of cells towards the upper surface, recorded in species of *Anodopetalum*, *Callicoma*, *Codia* (resembling stone cells), *Cunonia*, *Platylophus*, *Pullea*, *Weinmannia*. A tanniniferous hypoderm towards the lower surface recorded by Betts (187) in *Weinmannia racemosa* Linn. Cells of the epidermis and hypoderm provided with mucilaginous inner walls in all of the species examined. **Mesophyll** containing 'spicular cells' in *Pancheria* sp. Smaller **veins** vertically transcurrent or embedded. **Petiole**. Transverse sections through the distal end supplied by an almost continuous, adaxially flattened, cylindrical strand in *Cunonia capensis* Linn. (Fig. 126 c), but with the flat dorsal portion separated from the ventral arc. Structure somewhat similar in *Weinmannia trichosperma* (Fig. 126 B) but vascular strand continuous and rather different in shape. Small additional strands present in the wings in *Cunonia capensis*. Main vascular strand in both species strongly supported by a ring of pericyclic fibres. **Secretory cells** with amorphous, presumably tanniniferous contents present in the unligified tissues of the petiole in *Weinmannia trichosperma*; similar cells but with less definitely tanniniferous contents observed in the cortical and medullary regions of the petiole in *Cunonia capensis*. Solitary and clustered **crystals** common in the same 2 species.

AXIS

YOUNG STEM (Fig. 126 F)

Cork superficial, arising in the epidermis or sub-epidermis. **Cortex** somewhat spongy and composed of small cells in *Cunonia capensis* Linn. and *Weinmannia trichosperma* Cav. **Pericycle** containing a somewhat interrupted or continuous, sometimes composite ring of sclerenchyma. Secondary **phloem** including sclerosed cells in species of *Callicoma*, *Cunonia*, *Geissois*, *Pancheria*, *Weinmannia*. Phloem and **xylem** constituting continuous cylinders, traversed by narrow rays. Vessels observed to be angular and up to about 40 μ in radial diameter in *Cunonia capensis* and *Weinmannia trichosperma*. Exclusively scalariform perforation plates recorded in *Anodopetalum*, *Caldcluvia*, *Callicoma*, *Codia*, *Cunonia*, *Platylophus*, *Weinmannia* and mixed simple and scalariform plates in *Belangeria* and *Ceratopetalum*. Solereder records the occurrence of fibres with bordered pits in species of *Anodopetalum*, *Caldcluvia*, *Ceratopetalum*, *Cunonia*, *Pancheria*, *Platylophus*, and *Weinmannia*, and simple pits in *Belangeria*. **Pith** of *Cunonia capensis* and *Weinmannia trichosperma* quadrangular in transverse section, composed of cells larger in transverse diameter than those in other parts of the stem, many of them provided with pitted walls, mostly devoid of contents but some cells, filled with amorphous deposits, arranged in vertical columns. Other **secretory cells**, sometimes with mucilaginous contents, observed in the cortex, medullary rays, and pith of *Cunonia capensis*, and similar cells, but with apparently tanniniferous contents, in the phloem as well as the same tissues in *Weinmannia trichosperma*. Solitary and clustered **crystals** common in the unligified tissues.

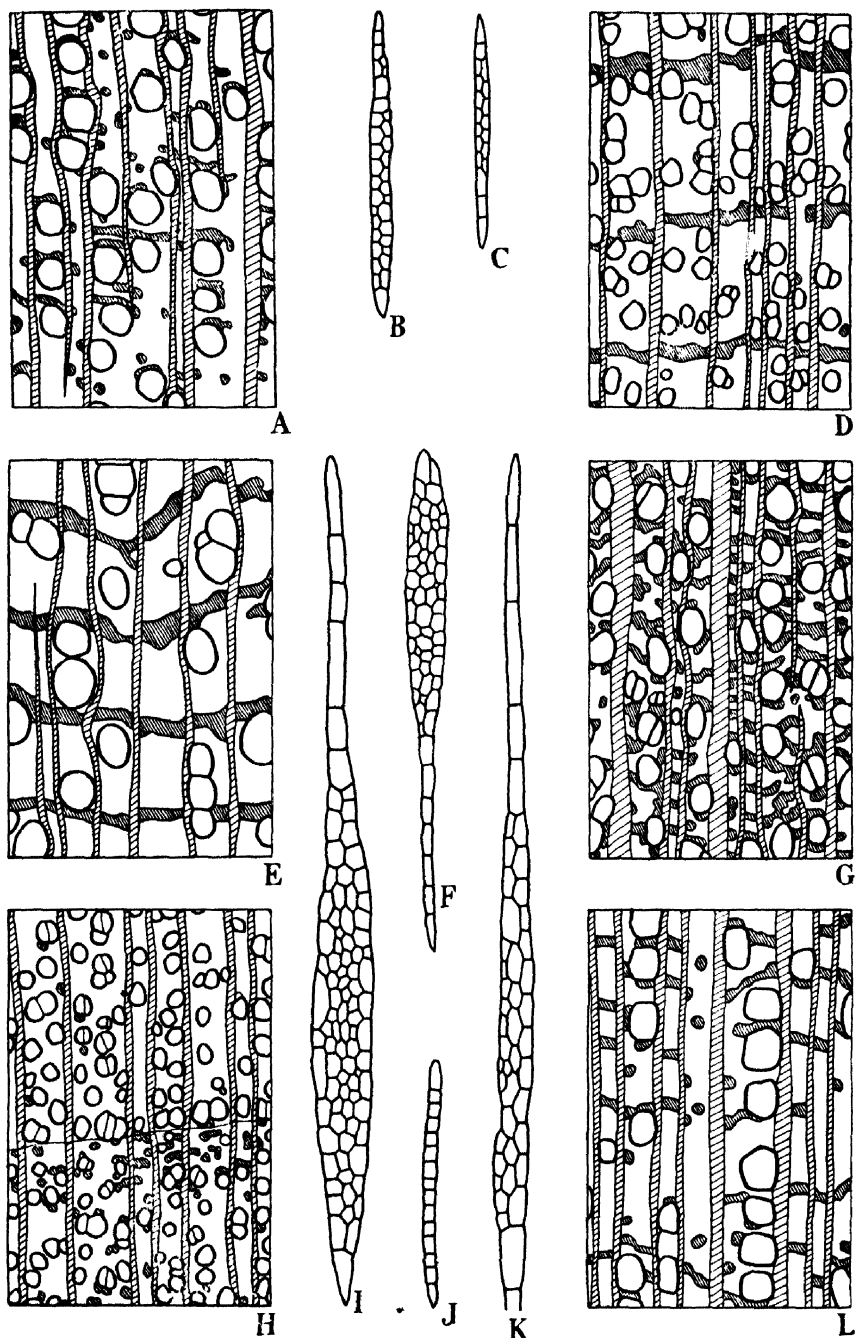


FIG. 125. CUNONIACEAE, A-G; EUCRYPHIACEAE, H-J;
 ESCALLONIACEAE, I and K-L

A, *Weinmannia blumei* Planch. B, *Platylophus trifolius* D. Don. C, *Ceratopetalum apetalum* D. Don. D, *C. apetalum* D. Don. E, *Schizomeria pulleana* O. Schmidt. F, *Cunonia capensis* Linn. G, *C. capensis* Linn. H, *Eucryphia lucida* (Labill.) Baill. I, *Quintinia sieberi* A. DC. J, *Eucryphia lucida* (Labill.) Baill. K, *Polyosma laete-virens* Griff. L, *P. laete-virens* Griff.

WOOD (Fig. 125 A-G)

Vessels typically moderately small (50–100 μ mean tangential diameter), slightly smaller in *Anodopetalum* and *Callicoma* (527) and rather larger in some species of *Ceratopetalum*, *Geissois*, and *Spiraeopsis*; solitary, apart from the apparent pairs produced by overlapping ends, in *Caldcluvia*, *Callicoma*, *Cunonia*, and *Weinmannia*, multiples of 2–3 cells common in the other genera, particularly in *Belangeria* (1886), *Geissois*, *Schizomeria*, and *Spiraeopsis*, with multiples of 2–9 cells in *Geissois* and *Schizomeria*, with a tendency to a tangential pattern in *Platylophus*; 8–130 per sq. mm., fewer than 20 per sq. mm. in *Geissois*, *Schizomeria*, and *Spiraeopsis*, about 100 per sq. mm. in *Anodopetalum*, *Caldcluvia*, *Callicoma*, and *Platylophus* (some specimens); semi-ring-porous in *Anodopetalum* and *Platylophus*. Perforation plates scalariform only and usually with fewer than 20 bars in *Ackama*, *Caldcluvia*, *Callicoma*, *Cunonia*, and *Weinmannia*,¹ with both simple and scalariform plates, the latter often limited to the smaller vessels, in *Anodopetalum*, *Belangeria* (2158), *Ceratopetalum*, *Geissois*, *Platylophus*, *Schizomeria*, and *Spiraeopsis*, with simple perforations only in some species of *Spiraeopsis*. Intervascular pitting predominantly scalariform in *Ackama*, *Anodopetalum*, *Caldcluvia*, and *Ceratopetalum*, opposite to alternate in *Geissois* and *Schizomeria*, intermediate between scalariform and opposite in the other genera; pits to ray and wood parenchyma typically large and horizontally elongated, sometimes exclusively circular in *Schizomeria*. Tyloses observed in *Caldcluvia*, *Platylophus*, *Spiraeopsis*, and *Weinmannia*. Mean member length 0.75–1.0 mm. **Parenchyma** apotracheal, as scattered cells (diffuse) in genera with solitary vessels, e.g. *Ackama*, *Caldcluvia*, *Callicoma*, *Cunonia* (some specimens) (Fig. 125 G), *Platylophus*, and *Weinmannia*, in numerous, irregular, uniseriate bands in *Anodopetalum*, *Cunonia*, *Geissois*, and *Spiraeopsis*, those of *Anodopetalum* almost entirely limited to the late wood; in wider and sometimes more regular bands 2–5 cells wide in *Ceratopetalum* and *Schizomeria* (Fig. 125 D–E), the short lines in *Weinmannia* and the broader bands in *Schizomeria* tending to be associated with the abaxial sides of the vessels (Fig. 125 A). Frequently with gummy contents; chambered crystals observed or reported in *Ackama* (525), *Caldcluvia*, *Callicoma* (2158), *Ceratopetalum*, *Cunonia* (2158), *Geissois*, *Spiraeopsis*, and *Weinmannia*. Strands usually of 4–8 cells. **Rays** of 2 distinct sizes in some genera, e.g. *Callicoma* and *Cunonia*, and with a tendency towards this in other genera; 2–4, occasionally 5, cells wide, seldom more than 1 mm. high except where there are 2 distinct multiseriate parts; exclusively uniseriate, according to Betts (188–9), in the shrubby *Weinmannia racemosa* Linn. F.; uniseriate rays numerous and composed of high upright cells in *Ackama*, *Callicoma*, *Cunonia*, and *Weinmannia*, the cells less high in the other genera and some of them procumbent in *Anodopetalum*, *Ceratopetalum*, *Platylophus*, *Schizomeria*, and *Spiraeopsis*; mostly 7–12 rays per mm.; more numerous (12–22) in *Caldcluvia*, *Callicoma*, *Geissois*, and *Platylophus*; heterogeneous (Kribs's Types I, II A and B), commonly with 4–10 marginal rows of upright cells except in *Anodopetalum*, *Ceratopetalum*, *Platylophus*, and *Schizomeria* p.p. Cells filled with gummy substance in many species,

¹ Dadswell and Eckersley (527) note that *Weinmannia lachnocarpa* F. v. M. differs from all other species of this genus in having simple perforation plates, alternate intervacular pitting, fibres with indistinctly bordered pits, and in some other respects.

crystals reported (527) in the upright cells of *Ackama*. **Fibres** with distinctly bordered pits, usually equally numerous on all walls, but sometimes more common on the radial walls, e.g. in *Schizomeria* and *Spiraeopsis*; Dadswell and Eckersley (527) describe the borders as small and inconspicuous in *Geissois* and *Schizomeria*. With thick walls in *Ackama*, *Anodopetalum*, *Cunonia*, and *Weinmannia*. Septate and with simple pits in *Belangera* (1886). Mean length 1.0–1.5 mm. **Pith flecks** common in *Geissois* (527).

ROOT

The occurrence of buttress roots has been recorded in *Ackama* and *Weinmannia* by Francis (707).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The spongy structure of the cortex, the characteristic quadrangular heterogeneous pith, and the tanniniferous secretions provide points of similarity between the Cunoniaceae and Eucryphiaceae, and thus tend to confirm the existence of affinities, which are suggested by the wood structure, between these two families. See also under 'Saxifragaceae'.

(ii) FROM WOOD STRUCTURE

Dadswell and Eckersley (527) suggest that *Weinmannia lachnocarpa* F. v. M. should be transferred to *Geissois* and note that *Geissois* and *Schizomeria* differ rather markedly from the rest of the family.

Tippo (2261) makes the following statement about the relative degree of specialization of the wood: 'The Cunoniaceae are on about the same level of development as are the Brunelliaceae. The former are lower in that all the species have tracheids, the vessel diameter is slightly smaller and two of the genera have exclusively scalariform plates. On the other hand, the Cunoniaceae have shorter vessel elements, the vessel member end-walls are less oblique and the rays are of higher type.'

Bausch (154) suggests that '*Platylophus* seems to be more typical of the Saxifragaceae', basing this on anatomy and chemical tests.

ECONOMIC USES

Coachwood, *Ceratopetalum apetalum* D. Don., and Red Els, *Cunonia capensis* Linn., are used in Australia and South Africa respectively for cabinet-work, and some of the other Australian genera provide wood that is used for tool handles, turnery, and other purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Anodopetalum, *Belangera*, *Caldcluvia*, *Callicoma*, *Ceratopetalum*, *Codia*, *Cunonia*,* *Geissois*, *Pancheria*, *Platylophus*, *Pullea*, *Weinmannia*.*

(ii) FOR WOOD STRUCTURE

Ackama, *Anodopetalum*, (*Belangera*), *Caldcluvia*, *Callicoma*, *Ceratopetalum*, *Cunonia*, *Geissois*, *Platylophus*, *Schizomeria*, *Spiraeopsis*, *Weinmannia*.

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Betts 187, Engler 638, Francis 707, Morvillez 1559.

(ii) *On Wood Structure*

Baker 104, Bausch 154, den Berger 179, 182, den Berger and Endert 183, Betts 188, 189, Chalk *et al.* 360, Dadswell and Eckersley 525, 527, Desch 574, Garratt 744, Howard 1088, Janssonius 1154, Record 1843, 1851, 1867-68, Record and Hess 1886, Record and Mell 1894, Scott 2075, Tippo 2261.

121. ESCALLONIACEAE

(FIG. 122 on p. 556; FIG. 123 on p. 558; FIG. 125 on p. 562)

SUMMARY

(i) GENERAL

A family of trees and shrubs which is widely distributed but occurs chiefly in the southern hemisphere, particularly in the Andes. The most interesting features recorded concerning the leaf are that the **stomata** are often provided with pairs of small guard cells, nearly circular in outline, whilst a **hypoderm** of 1-3 layers occurs in a number of genera. **Crystals** in both leaf and axis are predominantly clustered, although solitary types, crystal-sand, and styloids have also been reported. The nature and arrangement of sclerosed cells in the **pericycle** of the young stem are very variable. **Xylem**. Vessels in young stems of *Brexia*, *Escallonia*, and probably of other genera, small, angular; the perforations usually with scalariform plates except in *Brexia*.

(ii) WOOD

Vessels small and numerous, typically solitary, sometimes with numerous multiples and an oblique or radial pattern, occasionally ring-porous and with spiral thickening, perforation plates scalariform, intervacular pitting typically opposite, sometimes scalariform, pits to parenchyma similar; members of medium length to very long. **Parenchyma** apotracheal, diffuse. **Rays** up to 2-7 cells wide, markedly heterogeneous. **Fibres** with distinctly bordered pits, of medium length to moderately long.

LEAF

Dorsiventral in all species investigated. **Hairs** of several distinct types recorded or observed. (i) Unicellular, pointed, with moderately thick walls in *Escallonia*. (ii) Glandular, with short sunken stalks and unicellular heads in *Abrophyllum*. (iii) Glandular-shaggy, with multiseriate stalks of variable length and spherical or peltate heads in *Escallonia* (Fig. 123 D); particularly frequent on the leaf teeth of certain species. (iv) Peltate glands in *Quintinia*. (v) Two-armed in *Argophyllum*. **Cork warts**, not to be confused with glands, recorded on the leaf surface in one species of *Roussea*. **Stomata** with pairs of small guard cells nearly circular in outline in *Abrophyllum*, *Argophyllum*, *Escallonia*, *Itea*, *Quintinia*, *Roussea*; rubiaceous in *Quintinia*; with a double front cavity in *Brexia*. **Hypoderm** of 1-3 layers occurring on the upper side of the leaf in certain species of *Argophyllum*, *Carpodetus*, *Escallonia*, *Polyosma*, *Roussea*. **Mesophyll** including a single layer of palisade cells in *Abrophyllum*.

and *Argophyllum*. **Petiole.** Three vascular bundles enter the base in *Escallonia*. Transverse sections through the distal end exhibit a single, open, crescent-shaped bundle in *Escallonia macrantha* Hook. et Arn. and *E. rubra* (Ruiz et Pav.) Pers. (Fig. 122 B), accompanied by subsidiary strands in the wings in both species. Vascular structure in the petiole of *Brexia madagascariensis* Thouars (Fig. 122 C) with an abaxial crescent-shaped strand with incurved ends, accompanied by an additional small cylinder of xylem in the medullary region and 2 more dorsal ones. **Secretory cells** and cluster **crystals** present in the unligified tissues of the petiole of the same species and secretory cells only in *Escallonia macrantha*. Clustered crystals also recorded in *Anopterus*, *Carpodetus*, *Escallonia*, *Forgesia*, *Itea*, *Polyosma*; solitary and clustered ones in *Brexia* and *Quintinia*; crystal-sand in *Abrophyllum*.

AXIS

YOUNG STEM (Fig. 122 E)

Cork superficial in most members of the family, but arising in the pericycle, and composed of relatively thin-walled cells in species of *Escallonia*. **Cortex** containing slightly thickened sclerenchymatous cells in *Quintinia sieberi* A. DC.; with resin in the intercellular spaces in *Roussea*. Solereder notes the following types of sclerenchyma in the **pericycle** in at least certain species of the genera mentioned. (i) A composite and continuous ring of sclerenchyma in *Abrophyllum*. (ii) A ring of stone cells in *Polyosma*, *Quintinia*, *Roussea*. (iii) A ring of fibres in *Phyllonoma*. (iv) Isolated strands of fibres in *Anopterus* and *Itea*. (v) A composite and continuous ring or an interrupted ring of sclerenchyma in different species of *Brexia*. An interrupted or sometimes almost continuous ring of fibres was observed in the pericycle of species of *Brexia* and *Escallonia* examined at Kew. *Abrophyllum* differs from the other genera described in having, in the pericycle, a ring of laticiferous sacs, consisting of vertically elongated cells arranged in longitudinal rows and filled with white friable contents. **Phloem** and **xylem** in *Brexia madagascariensis* Thouars, *Escallonia macrantha* Hook. et Arn., and *E. rubra* (Ruiz et Pav.) Pers. constituting continuous cylinders traversed by narrow medullary rays; vessels small (radial diameter seldom exceeding $40\ \mu$), angular (less so in *Brexia* than in *Escallonia*). This structure is probably characteristic of other members of the family. Vessels exclusively with scalariform perforation plates in most investigated genera; mixed simple perforations and scalariform plates recorded in *Brexia*; only simple perforations seen in *B. madagascariensis* examined at Kew. **Pith** heterogeneous and somewhat spongy or becoming hollow; component cells abundantly pitted in *Escallonia rubra*. **Secretory cells**, with apparently tanniniferous contents, observed in the cortex, phloem, and medullary rays and pith of species of *Brexia* and *Escallonia*. **Laticiferous sacs**, see 'Pericycle'. **Crystals**, of the same types as those described under 'Leaf', occur also in the axis of the same genera; styloids also recorded in the phloem of *Escallonia*.

WOOD (Fig. 125 I, K, and L)

Vessels moderately to very small ($30\text{--}75\ \mu$ mean tangential diameter); typically solitary apart from the apparent tangential pairs produced by over-

lapping ends, but with numerous radial multiples and a tendency to a radial pattern in some species of *Polyosma* (Fig. 125 L), and with an oblique or radial pattern in *Itea* (1154, 1206); numerous, varying from about 20 per sq. mm. in some species of *Itea* (1206) and *Polyosma* to about 100 per sq. mm. in *Carpodetus* and *Escallonia* p.p.; semi-ring-porous and with spiral thickening in some species of *Escallonia*. Perforation plates typically scalariform, with both simple and scalariform plates in *Brexia* (2158, 2261); with less than 20 fine bars in *Carpodetus* and *Escallonia*, up to 40–70 bars in *Itea* (1154), *Polyosma* p.p., and *Quintinia*, and up to 125 bars in some species of *Polyosma* (1154); with reticulate plates in some species. Intervascular pitting scalariform in *Carpodetus* and *Itea* (1154, 1206), round and usually opposite in the other genera but with some transitional forms; pits to ray and wood parenchyma large and oblong in *Carpodetus* and *Itea* (1154), small, round, and similar to the intervacular pitting in the other genera; mean length 0.5–1.2, mostly more than 0.9 mm. **Parenchyma** exclusively apotracheal, as scattered cells (diffuse) with a tendency to form short uniseriate lines, e.g. in *Quintinia*, and sometimes more abundant near the vessels, e.g. in *Carpodetus*; in regular, multiseriate apotracheal bands in *Brexia* (2261). With chambered crystals in *Carpodetus* and *Brexia* (2261); sometimes filled with dark gum. Strands of 4–8 cells. **Rays** very variable in width in different species, tending to be of 2 distinct sizes; the larger rays up to 2–7 cells wide, widest in some species of *Escallonia* and *Polyosma*; exclusively uniseriate, at any rate in small material, in *Brexia* (2261); slightly more than 1 mm. in height in *Polyosma* and *Quintinia*; the uniseriate rays composed entirely of upright cells; 16–24 rays per mm. in *Carpodetus* and *Escallonia*, less numerous (about 10 per mm.) in *Polyosma* and *Quintinia*; heterogeneous (Kribs's Types I–II A and III in *Brexia*), with 4 or more marginal rows of square or upright cells and commonly with 10 or more rows in *Quintinia*; with sheath cells in *Escallonia* p.p. Sometimes with abundant gummy contents, e.g. in *Quintinia* and according to Tippe (2261) with crystals in *Brexia* and *Carpodetus*. **Fibres** with distinctly bordered pits, usually more numerous on the radial than on the tangential walls; walls moderately thick to thick; mean length 1.0–2.1 mm., longest in *Polyosma* (1154).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The nature of the stomata and the general structure of the young stem support the generally accepted view that the Escalloniaceae and Grossulariaceae are closely related. The stem of *Escallonia* and *Ribes* in particular are very much alike. The distinctive structure of the petiole of *Brexia* suggests that this genus may be rather remotely related to *Escallonia* and possibly to other genera in the family. See also under 'Saxifragaceae'.

(ii) FROM WOOD STRUCTURE

Tippe (2261) states:

'Anatomically the Escalloniaceae are very close to the Grossulariaceae. The former perhaps may be considered to be a little higher, for 1 genus in the Escalloniaceae has vessel elements with simple and rarely vestigial scalariform perforation

plates. On the other hand, the Grossulariaceae are more specialized in regard to certain other characters.'

'The three families Hydrangeaceae, Grossulariaceae and Escalloniaceae are very similar anatomically, but in general it may be said that the Hydrangeaceae are primitive, Grossulariaceae less so, and Escalloniaceae least primitive.'

Tippo (2261) considers the anatomy of the wood to be consistent with the derivation of the Cunoniales (including the Hydrangeaceae, Escalloniaceae, Cunoniaceae, Brunelliaceae, and Grossulariaceae) from the Magnoliales, and with the idea of the Cunoniales having given rise to the Rosales (including the Rosaceae and perhaps the Calycanthaceae). He notes trends towards the Rosales in the Hydrangeaceae, Grossulariaceae, and Escalloniaceae and considers that the last three groups could very well be placed in one family.

ECONOMIC USES

The family includes a number of ornamental shrubs commonly cultivated in gardens.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abrophyllum, Anopterus, Argophyllum, Brexia,* Carpodetus, Escallonia,* Forgesia, Itea, Phyllonoma, Polyosma, Quintinia, Roussea.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Brexia), Carpodetus, Escallonia, (Itea), Polyosma, Quintinia.

LITERATURE

(i) *On General Anatomy*
Engler 636.

(ii) *On Wood Structure*
den Berger 182, Desch 574, Janssonius 1154, Kanehira 1206, Record 1783, 1800, 1840, 1851, Record and Hess 1886, Tippo 2261, Welch 2401, Yamabayashi 2478.

122. EUCRYPHIACEAE

(FIG. 125 on p. 562; FIG. 126 on p. 570)

SUMMARY

(i) GENERAL

A family of trees and shrubs belonging to the single genus *Eucryphia* which occurs in Australia, Tasmania, and Chile. The following description of the leaf and young stem refers chiefly to *Eucryphia glutinosa* (Poepp. et Endl.) Baillon grown at Kew. This species has rubiaceous **stomata** whilst, in the young stem, the somewhat spongy **cortex**, the **xylem** with small vessels and uniseriate rays, the quadrangular heterogeneous **pith** and the occurrence of **tanniniferous elements** are useful diagnostic characters.

(ii) WOOD

Vessels small, mostly solitary, but with some multiples, spiral thickening sometimes present, perforation plates scalariform or scalariform and simple, intervacular pitting transitional between scalariform and opposite, pits to parenchyma often large, horizontally elongated and simple. Members of medium length to moderately long. **Parenchyma** apotracheal, diffuse to slightly banded, and sometimes in terminal bands. **Rays** exclusively uniseriate or 2-3 cells wide, heterogeneous. **Fibres** with bordered pits, of medium length.

LEAF

Leaflets dorsiventral. **Hairs** infrequent, but where present occurring in the form of short, unicellular, thick-walled trichomes. **Stomata** confined to the lower surface, $30\ \mu$ in diameter, mostly rubiaceous, with 1 or 2 pairs of subsidiary cells lying parallel to the pore. Subsidiary cells somewhat variable in shape, but many of them approximately rectangular. **Mesophyll** composed of 2 or 3 layers of palisade cells and of a region of spongy tissue, each occupying about half the thickness of the leaflet. Mesophyll cells, especially those of the palisade tissue, containing yellowish plastids. Vascular bundles of the smaller **veins** vertically transcurrent by sclerenchyma. **Petiole**. Transverse sections through the distal end in *Eucryphia glutinosa* Baill. exhibit, towards the abaxial side, a broad, crescent-shaped vascular strand, accompanied by a second bundle partially enclosed within but almost connected with the incurved ends of the first, the whole vascular system thus resembling a slightly interrupted, dorsally flattened cylinder (Fig. 126 A). Cortical parenchyma around the vascular strand very spongy. Numerous solitary and cluster **crystals** occur in the veins and, less frequently, in the mesophyll.

AXIS

YOUNG STEM (Fig. 126 D)

Cork superficial in material examined at Kew. **Cortex** somewhat spongy, composed mostly of small, sometimes pitted cells, but including a few branched, sclerenchymatous idioblasts. **Pericycle** bounded externally by a broad, almost continuous ring of thick-walled fibres with narrow lumina, locally interrupted by stone cells, the latter more numerous in \times *E. intermedia* Bausch than in *E. glutinosa* Baill. (Fig. 126 D). **Phloem** and **xylem** constituting continuous cylinders, traversed by narrow, almost exclusively uniseriate medullary rays. Phloem consisting wholly of soft tissue. Xylem vessels somewhat angular, seldom exceeding $30\ \mu$ in radial diameter; perforation plates scalariform or scalariform and simple. **Pith** approximately quadrangular in transverse section; very heterogeneous, composed of cells of much larger transverse diameter than any of those elsewhere in the stem; most of the cells thin-walled and devoid of contents, but others, often arranged in vertical columns, provided with thicker, pitted walls and filled with dense, amorphous, probably tanniniferous contents. Apparently tanniniferous cells also observed in the cortex, phloem, and medullary rays. **Crystals** not seen in *E. glutinosa*, but occasional solitary ones present in the cortex of \times *E. intermedia*, and more numerous solitary and clustered crystals in another, undetermined species of *Eucryphia*. **Secretory cells**, see 'Pith'.

Wood (Fig. 125 H and J)

Vessels very to moderately small, varying from about 30 to 70 μ mean tangential diameter, mostly about 60 μ (154); mostly solitary but with some

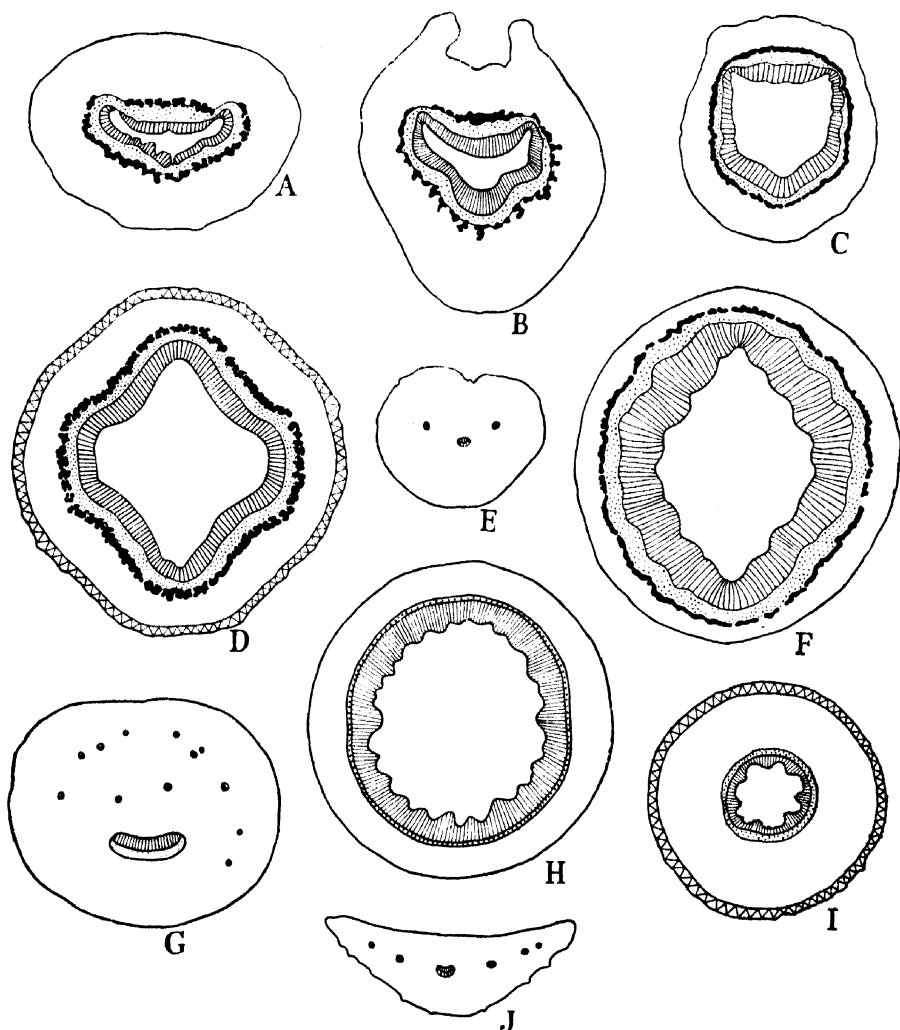


FIG. 126. *EUCRYPHIACEAE*, A and D; *CUNONIACEAE*, B-C and F; *CRASSULACEAE*, E and G-J

A, *Eucryphia glutinosa* Baill. Petiole $\times 19$. B, *Weinmannia trichosperma* Cav. Petiole $\times 33$. C, *Cunonia capensis* Linn. Petiole $\times 15$. D, *Eucryphia glutinosa* Baill. Stem $\times 19$. E, *Umbilicus pendulinus* DC. Petiole $\times 8$. F, *Cunonia capensis* Linn. Stem $\times 8$. G, *Bryophyllum daigremontana* Hamet et Perrier. Petiole $\times 8$. H, *B. daigremontana* Hamet et Perrier. Stem $\times 8$. I, *Sedum reflexum* Linn. Stem $\times 18$. J, *Crassula* sp. Petiole $\times 8$.

multiples and short chains, and with a slight tendency to tangential arrangement in some species; usually 70–120 per sq. mm., mostly about 100, reported by Vestal (2329) to be sometimes up to 200 per sq. mm.; with a tendency to

be semi-ring-porous in a few species; spiral thickening present in some species, absent from *Eucryphia cordifolia* Cav. (1886). Perforation plates typically all scalariform, but sometimes scalariform and simple, the multi-perforate plates usually with 20 or fewer bars but occasionally up to 40, and sometimes reticulate. Intervascular pitting transitional between scalariform and opposite. Pits to ray and wood parenchyma partly large, horizontally elongated and simple, and partly round and bordered, sometimes unilaterally compound. Thin-walled tyloses rarely present (154). Mean member length about 0.8 mm. **Parenchyma** predominantly apotracheal, as scattered cells (diffuse); tending to be more numerous and to form uniseriate lines in the late wood; sometimes in terminal bands 1-4 cells wide; Bausch (154) states that a small amount of paratracheal parenchyma is usually present. Cells commonly with dark gummy contents. Strands usually of 4-8 cells. **Rays** either exclusively uniseriate or up to 2-3 cells wide, and occasionally up to 4-6 cells wide in the middle (1886); 10-12 per mm.; heterogeneous (Kribs's Types II B and III), with 1-2 marginal rows of square to upright cells. Cells commonly filled with gummy or granular material. **Fibres** with distinctly bordered pits, equally numerous on both radial and tangential walls and in single rows; Bausch (154) describes the pits as inconspicuously bordered in some species. Walls usually thick, often differing markedly in the early and late wood. Mean length about 1.4 mm.

TAXONOMIC NOTES

Bausch (154) in a study of the affinities of the family states: 'The family is considered to be taxonomically most nearly related to the Cunoniaceae. This conclusion is based on morphological characters and on similarity of anatomical structure, especially on the occurrence of both simple and scalariform perforations in the vessels in the two families. Similarity in chemical properties also points to the same relationship.'

The features emphasized by Bausch in the wood anatomy do not necessarily imply relationship, nevertheless his general conclusion appears to be valid. Record and Hess (1886) also consider the wood anatomy to resemble that of the Cunoniaceae. For other points of similarity to Cunoniaceae see that family.

ECONOMIC USES

Leatherwood, *Eucryphia lucida* (Labill.) Baillon (syn. *E. billardieri* Spach.), is reported (525) to be used to a small extent for tool handles.

GENUS DESCRIBED

Eucryphia.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Bausch 154, Gilg 769.

(ii) *On Wood Structure*

Bausch 154, Dadswell and Eckersley 525, Record 1851, Record and Hess 1886, Record and Mell 1894, Vestal 2329.

123. GROSSULARIACEAE

(FIG. 122 on p. 556; FIG. 127 on p. 576)

SUMMARY

(i) GENERAL

A family of shrubs, mostly from north temperate regions; often with spines. The more important diagnostic characters include the small **stomata** which are nearly circular in outline; the deep-seated origin of the **cork**; the absence of **pericyclic sclerenchyma** from the young stem; in the **xylem** the small, angular vessels which nearly always have scalariform perforation plates.

(ii) WOOD

Vessels extremely small and very numerous, tending to form tangential lines, often ring-porous; perforations typically scalariform; intervascular pitting typically scalariform to opposite, pits to parenchyma similar; members of medium length. **Parenchyma** absent or in very rare bands. **Rays** up to 11-14 or more cells wide, heterogeneous. **Fibres** usually septate, very to extremely short. **Vascentric tracheids** present.

LEAF

Dorsiventral. **Hairs** mostly unicellular, but glandular, shaggy trichomes with multiseriate stalks of variable length and spherical or peltate heads also occur on the leaves and stipules. **Stomata** provided with pairs of small guard cells nearly circular in outline. **Petiole** examined in *Ribes aureum* Pursh., *R. grossularia* Linn., *R. nigrum* Linn., and *R. sanguineum* Pursh. (Fig 122 L) and the following structure observed. Three separate vascular bundles enter the base of the petiole, but transverse sections through the distal end exhibit a solitary crescent-shaped vascular strand, with the ends very much incurved and almost in contact with one another. Vascular strand in all four species supported by fibres in the pericyclic region. **Secretory cells** and clustered **crystals** fairly abundant in the parenchymatous tissues of the petiole.

AXIS

YOUNG STEM (Fig. 122 O)

Cork deep seated in origin; composed of thin-walled cells in at least certain species. **Pericycle** devoid of sclerenchyma. **Phloem** and **xylem** in some species, e.g. *R. grossularia* Linn., constituting almost or quite continuous cylinders traversed by narrow medullary rays, but with the xylem dissected by broader but lignified rays in other species, e.g. *R. aureum* Pursh. Vessels small and angular, e.g. up to about $36\ \mu$ in radial diameter in *R. nigrum* Linn. nearly always with scalariform perforation plates. **Pith** stellate in outline in *R. aurea* and *R. nigrum* but not in *R. grossularia*; commonly heterogeneous and frequently spongy. **Secretory cells** with apparently tanniferous contents common and frequently abundant in the cortex, phloem, medullary rays, and pith (usually arranged in vertical columns in the last of these tissues). Clustered **crystals** common in the unlignified tissues, but relatively infrequent in *R. nigrum*.

WOOD (Fig. 127 F-G)

Vessels extremely small (less than $25\ \mu$ mean tangential diameter) to very small ($25\text{--}50\ \mu$); with moderately numerous groups and tending to form a distinct tangential pattern in some species; very numerous, 100–300 per sq. mm.; ring-porous in some species. Perforation plates typically scalariform, with less than 20 thin bars, but Tipppo (2261) notes both simple and scalariform plates in one species. Intervascular pitting scalariform to opposite, rarely alternate (2261); pits to wood and ray parenchyma similar in size and shape to the intervascular pitting. Mean member length 0.36–0.66 mm. (2261). **Parenchyma** typically very rare or absent; Tipppo (2261) reports the rare occurrence of apotracheal bands 1–6 cells wide. **Rays** of 2 distinct sizes, the larger up to 11–14 cells wide and occasionally up to 22 cells (2261); up to about 1 mm. high; uniseriate rays numerous, low, and composed entirely of square or upright cells; rays 10–14 per mm.; heterogeneous (Kribs's Type II A), with 1–3 marginal rows of upright cells, commonly with sheath cells. **Fibres** usually septate, the septa rare in some species; pits with very narrow borders; walls moderately thin to moderately thick; mean length about 0.5 mm. **Vasicentric tracheids** present.

TAXONOMIC NOTES, *see under* Saxifragaceae and Escalloniaceae

ECONOMIC PRODUCTS

Gooseberries (*Ribes grossularia* Linn.), Black Currants (*R. nigrum* Linn.), and Red Currants (*R. rubrum* Linn.) are well-known edible fruits, selected varieties of which are commonly cultivated. Other species, e.g. *R. sanguineum* Pursh., are cultivated on account of their ornamental flowers.

GENUS DESCRIBED

Ribes.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Engler 636, Morvillez 1559.

(ii) *On Wood Structure*

Baker 104, Chalk and Chattaway 358, Cozzo 494, Greguss 2522, Record 1843, 1851, Record and Hess 1886, Tipppo 2261, Welch 2401.

124. HYDRANGEACEAE

(Fig. 122 on p. 556; FIG. 123 on p. 558; FIG. 127 on p. 576)

SUMMARY

(i) GENERAL

A family of trees and shrubs from north temperate and sub-tropical regions. One of the most interesting anatomical features is the common but not universal occurrence of **raphide sacs**, which also contain mucilage, in both leaf and axis. In the leaf they are usually to be found in the spongy mesophyll

where they lie parallel to the surface of the leaf, but they also occur in the palisade tissue. In the axis they are present in the cortex, phloem, and pith. A **hypoderm** of 1–3 layers is common in some of the genera. The **cork** in the young stem is sometimes differentiated into alternating rows of cells which are radially elongated and radially compressed respectively. A characteristic ring of stone cells is present immediately within the cork cambium, in certain genera. In the **xylem** the vessels mostly have exclusively scalariform perforation plates, although simple ones are sometimes to be found amongst them.

(ii) WOOD

Vessels small, numerous and solitary, commonly semi-ring-porous and with spiral thickening, perforation plates typically scalariform with numerous fine bars, rarely simple, intervascular pitting scalariform to opposite, pits to parenchyma similar to the intervascular pitting, moderately to very long. **Parenchyma** absent, diffuse or scanty paratracheal. **Rays** 2–9 cells wide, heterogeneous. **Fibres** typically with numerous bordered pits, rarely septate, with spiral thickening in 2 genera, very long.

LEAF

Dorsiventral in all the species investigated. **Hairs**. Simple, unicellular, papillose trichomes observed in *Philadelphus* (Fig. 123 A), the frequency and length varying in different species; very long unicellular trichomes present in *Jamesia americana* Torr. et Gray; tufted in *Broussaisia* and *Pileostegia* (with calcified walls); stellate (Fig. 123 B–C), calcified, unicellular types occur in species of *Deutzia*. **Leaf teeth** sometimes glandular in *Decumaria*, *Deutzia*, *Philadelphus*. **Epidermis** locally consisting of horizontally divided cells in *Carpenteria*. **Hypoderm** of 1–3 layers on the upper side of the leaf recorded in 1 species of *Broussaisia* and in *Hydrangea* (pro parte). **Stomata** rubiaceous in certain species of *Dichroa* and *Hydrangea*; ranunculaceous in *Philadelphus*. **Mesophyll** including 1 layer of palisade tissue in *Deutzia* and *Philadelphus*. **Petiole**. Transverse sections through the distal end exhibiting an open, crescent-shaped vascular strand in species of *Deutzia* (Fig. 122 A), *Jamesia*, and *Philadelphus*. Vascular strand crescent-shaped but less open and usually somewhat dissected in species of *Hydrangea* (Fig. 122 D) and *Pileostegia*. Main strand consisting of an abaxial arc with a separate, flat, adaxial bundle between the ends in *Decumaria sinensis* Oliv., *Dichroa febrifuga* Lour., and *Hydrangea petiolaris* Sieb. et Zucc. (Fig. 122 F). Additional strands present in the wings in the same species of *Decumaria*, *Dichroa*, and *Pileostegia* and in the medullary region in *Hydrangea* and *Pileostegia*. **Secretory cells**, with unidentified amorphous contents, observed in the unlignified tissues of the petiole in *Decumaria*, *Deutzia*, *Dichroa*, *Hydrangea*, *Jamesia*, and *Pileostegia* but not in *Philadelphus*. **Raphide sacs** (see also 'Young Stem') containing mucilage common; usually lying in the spongy mesophyll parallel to the surface of the leaf, but sometimes amongst and parallel to the palisade cells; occasionally visible as transparent dots in *Decumaria*. Similar secretory sacs, but with grey, finely divided contents, observed in addition to ordinary raphide sacs in *Pileostegia viburnoides* Hook. f. et Thoms. Clustered **crystals** present in *Carpenteria*, *Dichroa*, *Jamesia*, *Philadelphus*.

AXIS

YOUNG STEM (Fig. 122 G-H)

Cork deep seated in origin in species of *Deutzia*, *Hydrangea*, *Jamesia*, *Pileostegia* examined at Kew; consisting of rows of radially elongated cells alternating with radially compressed cells in *Jamesia*, *Philadelphus* (radially compressed cells sometimes sclerotic); some of the cells provided with horse-shoe-shaped thickenings in *Whipplea*. A ring of stone cells on the inside of the cork cambium recorded in species of *Broussaisia*, *Decumaria*, *Pileostegia*, *Schizophragma*; sclerenchymatous elements also observed in the same position in species of *Decumaria* and *Philadelphus*. **Pericycle** devoid of sclerenchyma in at least certain species of *Decumaria*, *Deutzia*, *Hydrangea*, *Jamesia*, *Philadelphus*, *Pileostegia*. **Phloem** usually in the form of a rather broad, continuous cylinder, consisting of unligified tissue. **Xylem** also cylindrical and traversed by narrow rays in certain species of *Decumaria*, *Deutzia*, and *Pileostegia*, but dissected by broader, lignified rays in species of *Deutzia*, *Hydrangea* (Fig. 122 H), *Jamesia*, *Philadelphus* (Fig. 122 G). Vessels small, none seen to be more than about $50\ \mu$ in radial diameter in the material available for examination, frequently angular. Perforation plates exclusively scalariform in *Broussaisia*, *Decumaria*, *Deutzia*, *Dichroa*, *Fendlera*, *Hydrangea*, *Jamesia*, *Philadelphus*, *Pileostegia*, *Platycrater*, *Schizophragma*; simple and scalariform types recorded in *Cardiandra* and *Whipplea*. **Pith** usually large in proportion to the diameter of the stem, consisting mostly of thin-walled tissue, without contents apart from a narrow perimedullary zone of cells with thicker walls; tending to break down and become hollow, e.g. in *Deutzia*. Pith of the type just described observed in species of *Deutzia*, *Hydrangea*, *Jamesia*, *Philadelphus*; smaller and composed of spongy tissue in *Hydrangea petiolaris* Sieb. et Zucc. and *Pileostegia viburnoides* Hook. f. et Thoms. **Raphide sacs** (see also 'Leaf') containing mucilage said to be very common in the primary cortex, phloem, and pith; but none were observed in species of *Deutzia*, *Jamesia*, and *Philadelphus* although seen in species of *Decumaria*, *Hydrangea*, and *Pileostegia*, those of *P. viburnoides* much elongated and filled with an orange secretion. The distribution of raphide sacs in the different tissues varies according to the species. **Secretory cells** with unidentified, amorphous contents observed in the parenchymatous tissues in species of *Decumaria*, *Deutzia* (pro parte), *Hydrangea*, *Pileostegia*; none seen in *Philadelphus*. Elongated secretory sacs, resembling the raphide sacs but filled with a finely divided greyish substance, observed in the phloem of *Decumaria sinensis* Oliv.

WOOD (Fig. 127 A-E)

Vessels small (less than $100\ \mu$ mean tangential diameter), ranging from $25\ \mu$ in some species of *Deutzia* to about $60\ \mu$ in *Philadelphus* in the material examined; Tippon (2261) gives the range as $22-130\ \mu$; typically solitary, apart from the apparent tangential pairs produced by overlapping ends, but with moderately numerous multiples in *Deutzia glabrata* Komorow; very numerous, ranging from 40 to over 200 per sq. mm.; ring-porous or semi-ring-porous in some species of *Deutzia*, *Fendlera* (1864), *Hydrangea*, and *Philadelphus* and with spiral thickening in some species of *Deutzia*, *Hydrangea* (1851), and

Philadelphus. Perforation plates typically all scalariform, with 20-90 fine bars, but all, or predominantly, simple in *Deutzia glabrata* and some species of *Philadelphus* (2478); Solereder, quoting Halle, notes both simple and

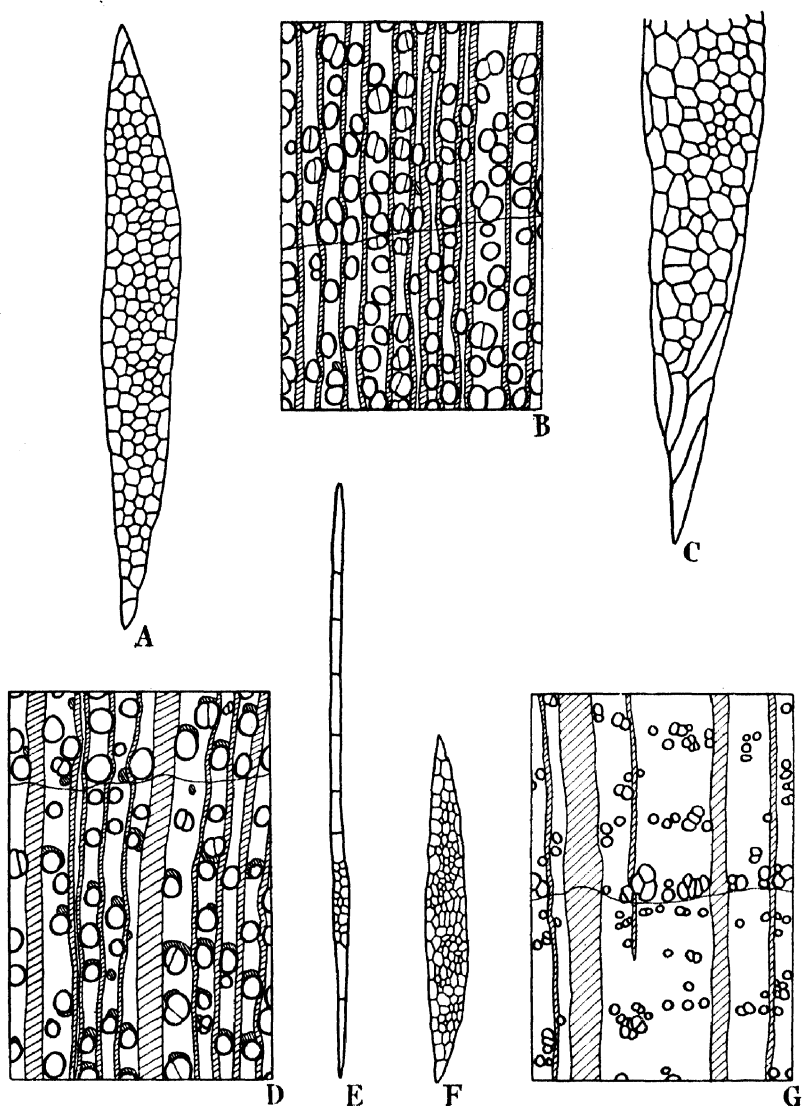


FIG. 127. HYDRANGEACEAE, A-E; GROSSULARIACEAE, F-G

A, *Philadelphus incanus* Koehne. (Not entirely typical; most rays distinctly heterogeneous.) B, *Hydrangea bretschneideri* Dippel. C, *Deutzia scabra* Thunb. D, *Philadelphus incanus* Koehne. E, *Hydrangea bretschneideri* Dippel. F, *Ribes glaciale* Wall. G, *R. glaciale* Wall.

scalariform plates in *Cardiandra* and *Whipplea*. Intervascular pitting scalariform in *Dichroa* (1154), *Hydrangea*, and *Schizophragma*, opposite in *Deutzia* p.p. and *Philadelphus*, alternate in *Deutzia glabrata*; pits to ray and wood

parenchyma similar to the intervacular pitting, large and oblong in *Dichroa* (1154), *Hydrangea*, and *Schizophragma*, small and round in *Deutzia* and *Philadelphus*. Tyloses reported by Tippo in a single species. Mean member length 0.56–1.35, mostly above 1.0 mm. **Parenchyma** diffuse in *Deutzia*, predominantly paratracheal (scanty), but with a few scattered cells in *Philadelphus*, absent or with a few cells round the vessels in *Dichroa* (1154), *Hydrangea*, and *Schizophragma*. Strands of 6–8 cells. **Rays** tending to be of 2 distinct sizes; up to 2–3 cells wide and less than 1 mm. high in some species of *Deutzia* and *Hydrangea*, up to 4 or more cells wide in other species and in *Philadelphus* and *Schizophragma*, and up to 9 cells in *Hydrangea* p.p. (1206); more than 1 mm. high in *Deutzia* p.p., *Philadelphus*, and *Schizophragma*; uniseriate rays numerous and composed entirely of high upright cells; rather fewer in *Philadelphus* and *Schizophragma*; about 30 rays per mm. in *Deutzia* and *Hydrangea*, distinctly fewer (about 10 per mm.) in some species of *Philadelphus* and *Schizophragma*. Heterogeneous (Kribs's Type I), with 4–10 marginal rows of upright cells; usually with sheath cells. **Fibres** typically with small to large bordered pits, often very numerous on both radial and tangential walls; but with simple pits in *Deutzia* p.p., *Dichroa*, and some species of *Hydrangea* (1206) and septate according to Kanehira (1206) in *Deutzia* p.p., *Dichroa* (1154), and *Hydrangea*; walls moderately to very thick, with spiral thickening in *Deutzia* and *Philadelphus coronarius* L. (2158). Mean length 1.1–1.6 mm.

TAXONOMIC NOTES, *see under* Saxifragaceae and Escalloniaceae

ECONOMIC USES

The family includes many well-known ornamental shrubs.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Broussaisia, Cardiandra, Carpenteria, Decumaria,* *Deutzia*,* *Dichroa*,* *Fendlera*, *Hydrangea*,* *Jamesia*,* *Philadelphus*,* *Pileostegia*,* *Platycrater*, *Schizophragma*, *Whipplea*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(*Cardiandra*), *Deutzia*, (*Dichroa*), (*Fendlera*), *Hydrangea*, *Philadelphus*, *Schizophragma*, (*Whipplea*).

LITERATURE

(i) *On General Anatomy*

Engler 636, Morvillez 1559.

(ii) *On Wood Structure*

Greguss 2522, Kanehira 1206, 1209, Janssonius 1154, Record 1783, 1800, 1840, 1851, 1864, Tippo 2261, Yamabayashi 2478.

125. CRASSULACEAE

(FIG. 124 on p. 558; FIG. 126 on p. 570)

SUMMARY

A family from warm dry regions, consisting mainly of succulent herbs, but tending to be miniature shrubs or trees in certain genera and species. Most members of the family are remarkable for their xeromorphic structure, particularly the occurrence of water-storage tissue in the leaf and stem. Some are believed to be capable of absorbing water directly from the air by special hairs, epidermal cells, or adventitious roots (Marloth 1445 and Berger 176). Kean (1224) concluded that the hydathodes (see below) of *Rochea coccinea* (L.) DC. serve solely for the secretion and not for the absorption of water, whilst the bladder hairs of *Crassula falcata* Wendl. (syn. *Rochea falcata* DC.) can take up moisture from the atmosphere. Reiche (1907) has pointed out that the vascular strands are widely and irregularly distributed throughout the water-storage tissue of numerous species, and he likens the vascular system of the Crassulaceae, embedded in aqueous tissue, to water plants whose finely divided members are suspended in a fluid medium. Reiche terms succulent plants which exhibit this structure 'innere Wasserpflanzen'. The **stomata** are nearly always surrounded by a girdle of 3 subsidiary cells and occur on all parts of the surface of the leaf. The leaves are frequently centric, and typical palisade tissue is rare. The fleshy structure of the stem is due to the well-developed parenchymatous or collenchymatous tissues of the **cortex** and **pith**. **Secretory cells**, with contents generally described as tanniniferous, are common in the same tissues and in the phloem. The **xylem** in the stem is very seldom dissected by wide rays, and there is a considerable range of variation in the distribution of the vessels. **Cortical bundles**, which represent leaf traces, are common; **medullary bundles** and **anomalous structure** have been recorded and described in a few genera and species. A red **anthocyan pigment**, the colour of which is intensified by bright light, is common in many members of the family, either throughout the plant or localized in certain organs or parts of organs in different species. Certain species of *Bryophyllum*, notably *B. pinnatum* (Lam.) S. Kurz (syn. *B. calycinum* Salisb.) and *B. daigremontianum* R. Hamet et Perrier (syn. *Kalachoe daigremontiana* R. Hamet et Perrier), are remarkable for the fact that they reproduce vegetatively by means of foliar embryos which arise in notches in the leaf margins. This method of reproduction has been the subject of numerous anatomical and physiological investigations. For particulars concerning a selection of these see Johnson (1186), Mehrlich (1479), Sobels (2156), Yarbrough (2483, 2484).

LEAF

Usually centric or intermediate between dorsiventral and centric; typical palisade tissue rare. **Hairs** usually infrequent, but several kinds recorded. (i) Bladder-like hairs, sometimes described as epidermal cells, present in *Crassula falcata* Wendl. (Fig. 124 B-C) (covering the whole surface) and *Rochea coccinea* (L.) DC. (confined to the leaf margins) (Lindinger 1374 and Rehfoos 1904); similar structures also observed in an unidentified species of

Crassula examined at Kew. (ii) Glandular hairs, with short or long stalks and which sometimes secrete mucilage, recorded in species of *Aeonium*, *Cotyledon*, *Echeveria*, *Kalanchoë* (glands red in *K. aromatica* Perrier), *Sempervivum*. (iii) Three-armed, pointed hairs present in *Kalanchoë* section *stellatopilosae*, e.g. *K. beharensis* Drake according to Berger (176). (iv) Biseriate hairs forming a cobweb-like surface to the leaf, together with transitions between these and glandular shaggy types, present in *Sempervivum arachnoideum* Linn. Leaf surface often covered by a bluish-white coating of **wax** secreted from the epidermis. **Epidermis** (Fig. 124 D) usually composed of cells elongated transversely to the longitudinal axis of the leaf; papillose in a few species of *Bryophyllum* and *Sedum*. Papillae of a special type, each with a central perforation of the cuticle, a central reduction of the outer wall, and a mucilaginous protoplast recorded by Sporer (2171) at the margins of the leaf of the xerophytic *Crassula pyramidalis* Thunb. Epidermis occasionally 2-layered in the same genera. **Stomata** present on all parts of the surface of the leaf; surrounded by a girdle of 3 subsidiary cells, e.g. in *Crassula muscosa* (L.) Roth. (syn. *Tillaea muscosa* Linn.) and *Sedum spurium* Marsch-Bieb (Fig. 124 A). **Hydathodes**, which appear as small pits or spots on the leaf visible to the naked eye, are variously distributed in different species, sometimes covering the whole of both surfaces, at others confined to one surface or arranged in rows near the leaf margin on both surfaces or only on the lower side. Hydathodes recorded in species of *Bryophyllum*, *Crassula*, *Kalanchoë*, *Sedum*, *Umbilicus*; appearing as red-coloured pores on the upper surface in *Crassula schmidtii* Regel according to Weingart (2380). Transverse sections through the distal end of the **petiole** (Fig. 126 E and J) exhibiting, in most of the few species examined, an open arc or crescent consisting of a variable number of collateral bundles of which the median one is larger or much larger than the remainder. Median vascular strand accompanied by numerous smaller ones in the cortical region in *Bryophyllum daigremontianum* R. Hamet et Perrier (Fig. 126 G). **Secretory cells**, with apparently tanniniferous contents, common in unligified tissues, especially around the veins; only rarely morphologically differentiated from neighbouring cells. **Crystals** common, solitary, clustered, or in the form of sphaerites and crystal-sand.

AXIS

STEM (Fig. 126 H-I)

Cork, usually consisting of thin-walled cells, arising in the epidermis in *Bryophyllum* and *Sedum*, but sometimes sub-epidermal or even more deeply seated in other genera; described by Heckel (928) and Jadin and Juillet (1139) as becoming impregnated with resin and forming a thick layer capable of reducing evaporation in certain species of *Kalanchoë* from Madagascar. Heckel draws attention to the similarity between the resinous cork of these species of *Kalanchoë* and that of *Sarcocaulon* (Family Geraniaceae). **Cortex** well developed, fleshy; consisting wholly of parenchyma or with the outer part collenchymatous. Centric, sometimes numerous **cortical bundles** (leaf traces) with central xylem present in certain species of *Aeonium*, *Greenovia*, *Rochea*; similar bundles also recorded by Dauphiné and Hamet (549) and Dauphiné (547) in species of *Cotyledon* and *Kalanchoë*. **Phloem** poorly developed, including narrow sieve tubes which are not easily seen. **Xylem**

nearly always in the form of a continuous cylinder, only rarely dissected by wide rays, but exhibiting the following varied types of structure in species with a well-developed axis. (i) Forming a closed ring, consisting wholly of prosenchyma and without vessels (apart from those in the primary xylem) or rays, situated on the outside of the primary groups of vessels in species of *Sedum* and *Umbilicus*. (ii) Similar to (i) but small groups of vessels accompanied by elongated, unligified, parenchymatous cells, included in the ring, in species of *Aeonium*, *Bryophyllum*, *Crassula*, *Echeveria*, *Sedum*. (iii) As (ii) but with the groups of vessels and accompanying unligified parenchyma larger and arranged in concentric circles, in species of *Cotyledon*, *Crassula*, *Kalanchoë*, *Rochea*, and *Sempervivum*. (iv) Groundwork of the xylem in *Crassula argentea* Thunb. consisting of unligified tissue with vessels irregularly distributed in it, the vascular tissues being in the form of bundles separated from one another by primary rays. Vessels of the secondary xylem with simple pits or reticulate thickening, bordered pitting not recorded; perforations simple. Jeffrey and Cole (1167) record that some of the so-called vessels of the Crassulaceae resemble tracheids, since their terminal pores are occluded. Growth rings not well defined. Cambial activity not very considerable even in species with relatively wide stems; secondary growth in thickness stated to occur through cell divisions in the cortex and pith, e.g. in species of *Bryophyllum* and *Crassula*. **Medullary bundles** first recorded in the flower stalk of *Greenovia* by Hamet (875, 876), but subsequently noted by the same author in *Echeveria* as well (877, 878). Medullary bundles of *Echeveria minutiflora* Rose (syn. *Thompsonella minutiflora* Britton et Rose) differ from those of other species of *Echeveria* and from *Greenovia* (i) in being more remote from and not connected with the main vascular ring; (ii) in developing considerably later than instead of at the same time as the main vascular system. **Secretory cells**, with contents presumed to be tanniniferous, common in the unligified tissues; sometimes sufficiently elongated to be described as sacs and arranged in longitudinal series. **Developmental anatomy**. Maas (1405) studied the developmental anatomy of the stem of various species of *Crassula*, and found considerable variations in different species.

ANOMALOUS STRUCTURE

The complex anomalous structure of old stems of *Sedum populifolium* Pall. is described by Solereder as follows:

'The young stem of this species, externally to the primary groups of vessels, contains a ring of wood fibres, enclosing isolated vessels only. Subsequently the cambium produces, in the first place, a ring of thin-walled tissue with groups of vessels, which lie on the same radii as the primary vessels; but this is followed by a second ring of fibres, which only differs from the first in having more numerous groups of vessels embedded in thin-walled tissue, and so on. The ring of thin-walled tissue, which succeeds the first ring of fibres, soon becomes filled with contents, and assumes the appearance of a pith; its innermost layer of cells develops into a cork cambium, and the cork-tissue derived from the latter shuts off all the tissue lying internally to it (pith, primary groups of vessels and the first ring of fibres) from the outer woody tissue. The phenomena described are repeated. In each period of vegetation a new ring of wood is developed, and begins with a zone of thin-walled tissue; and similarly in the innermost cell layer of these zones successive layers of cork are formed.'

Anomalous structure also recorded in the rhizome of *Sedum aizoon* Linn. and other species of *Sedum* possessing rhizomes of a similar type. For details see Pfeiffer (1712). The middle part, but not the two ends, of the napiform roots of *Sedum* section *Telephium* also exhibits anomalous structure described by Solereder as follows:

'In transverse section this region shows a circle of concentric vascular bundles with central wood. Originally the fibro-vascular system of the roots possesses normal structure as Koch was the first to show. Subsequently, however, the ring of cambium breaks up into a number of separate arcs, which extend round portions of the original xylem and enclose them in an annular manner.'

ROOT

Most members of the family are described by Molisch (1549) as having red root tips, coloured by an **anthocyan pigment**, e.g. in certain species of *Echeveria*, *Kalanchoë*, *Sedum*, *Sempervivum*, but red tips not observed by the same author in certain species of *Bryophyllum*, *Cotyledon*, *Crassula*. Dried and fresh adventitious roots form a reddish felt on the stemlets of *Adromischus* spp. For the abnormal structure of the roots of *Sedum* section *Telephium* see 'Anomalous Structure' above.

ECONOMIC USES

Many members of this family are cultivated for ornamental purposes or because of their curious habit. Gyr (855) has recently described the anatomy of 6 species of *Sedum* which are used in folk medicine.

GENERA DESCRIBED

Adromischus, *Aeonium*, *Bryophyllum*,* *Cotyledon*, *Crassula*,* *Echeveria*, *Greenovia*, *Kalanchoë*,* *Rochea*, *Sedum*,* *Sempervivum*,* *Tillaea*, *Umbilicus*.*

* Represented in the Kew slide collection.

(So far as possible the synonymy in Berger's (176) monograph has been adopted.)

LITERATURE

On General Anatomy

Berger 176, Cholodny 406, Dauphiné 546, 547, Dauphiné and Hamet 549, Gyr 855, Hamet 875, 876, 877, 878, Heckel 928, Jadin and Juillet 1139, Jeffrey and Cole 1167, Johnson 1186, Kean 1224, 1225, 1226, 1227, Lindinger 1374, Maas 1405, Marloth 1445, Mehrlich 1479, Meyer 1508, Molisch 1549, Pfeiffer 1712, Rehous 1906, Reiche 1907, Sobels 2156, Sporer 2171, Weingart 2388, Yarbrough 2483, 2484, Zemke 2505.

126. DROSERACEAE

(FIG. 128 on p. 582; FIG. 129 on p. 584)

SUMMARY

The morphology and biology of members of this widely distributed family, many of which occur in boggy localities, have been described very completely by Diels (586) and Lloyd (1383). There is, therefore, no need to deal with them in great detail here, and it will suffice to give a brief résumé

of such facts concerning their anatomy as have been recorded or observed. The family consists of small shrubs with leaves bearing glandular hairs, some of which secrete substances which ensnare and digest insects and other small animal organisms. Since the morphology and anatomical structure of the plants differ somewhat, each of the genera is described separately below.

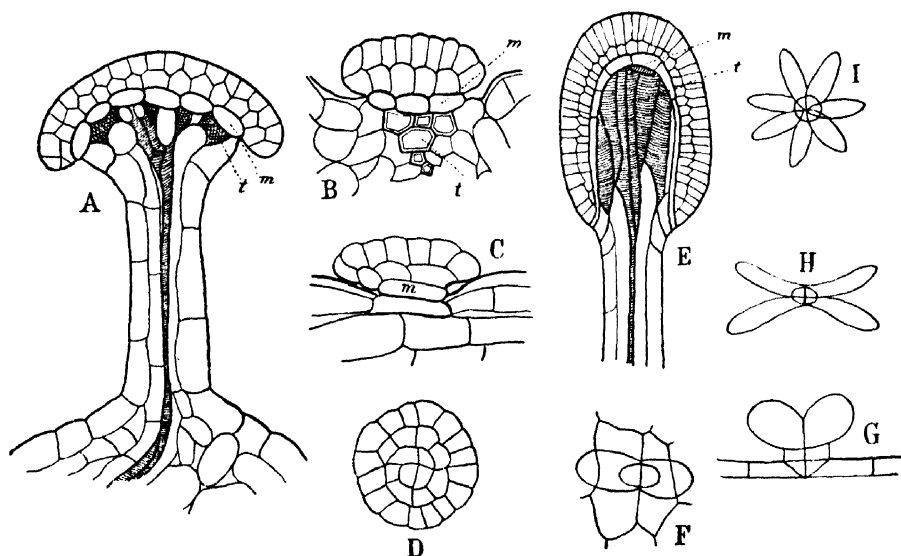


FIG. 128. DROSERACEAE

A, Longitudinal section through a glandular tentacle of *Drosophyllum lusitanicum* Link. B, A similar section through a shortly stalked gland of *Drosophyllum*. C, Longitudinal section through the glandular disk of *Dionaea muscipula* Ellis. D, Surface-view of the same gland. E, Longitudinal section through a glandular tentacle from the upper side of the leaf of *Drosera rotundifolia* Linn. F, Two-armed hair of *Aldrovanda vesiculosa* Linn. G, Glandular hair of *Drosera rotundifolia*. H, Four-rayed hair of *Aldrovanda*. I, Stellate hair of *Dionaea*.—A–C after Goebel, D and J after Fraustadt, E after de Bary, F and H after Caspary, G after Nitschke.

(m = Middle layer, t = Tracheids.)

DROSER (Sundews)

Terrestrial herbs with a basal rosette of red leaves. **Tentacles** (Fig. 128 E) present on the margin and upper surface of the leaf; each consisting of a stalk of varied length, traversed longitudinally by fine tracheids terminating in large groups in the heads. Outer part of the heads of the tentacles composed of 2 external layers of glandular cells surrounding a suberized or cutinized layer. Dome-shaped **sessile glands** (Fig. 128 B–D), often filled with a red or purple fluid, also present on both surfaces of the leaf, as well as on the stalks of the tentacles. Structures transitional between tentacles and sessile glands recorded in certain species. **Stomata** present on both surfaces. **Mesophyll** of *D. rotundifolia* Linn. composed of uniform, spongy tissue consisting of round cells. Vascular bundles of the **veins** in the same species embedded in the mesophyll and surrounded by a more or less definite sheath of parenchymatous cells. Structure similar in *D. binata* Labill., but central part of the mesophyll consisting of larger cells than those towards the 2 sur-

faces; chlorophyll granules much more numerous in the small outer than in the large central cells. Transverse sections through the distal end of the **petiole** of *D. rotundifolia* Lin. (Fig. 129 B) exhibit about 3 widely spaced vascular bundles, not accompanied by sclerenchyma, but each including well-developed phloem and a few small xylem vessels. Petiole of *D. binata* Labill. (Fig. 129 A) supplied by 2 much longer, cylindrical vascular bundles. **Scape** of the same species (Fig. 129 F) with a narrow cortex, bounded internally by a broader, well-defined, mechanical ring of elongated, relatively thick-walled cells; a circle of vascular bundles tending to be centric in structure and including very few vessels; a large, slightly spongy pith, composed of thin-walled, somewhat elongated cells. In the **root**, according to Solereder, the cortical parenchyma is composed of spirally thickened cells with wide lumina in certain species; the vascular bundles often being centric with central phloem and arranged in a simple or multiple ring or irregularly distributed in the ground tissue.

DROSOPHYLLUM

The following description applies particularly to *D. lusitanicum* (L.) Link. General morphology similar to that of *Drosera* but taller, tending to be almost shrubby. **Tentacles** and **glands** (Fig. 128 A-D) not unlike those of *Drosera*. **Mesophyll** composed of uniform spongy tissue, but with very much larger intercellular spaces than in either of the species of *Drosera* described. Vascular bundles of the **veins** also larger than those of *Drosera*, the one in the midrib being supported by a wide sheath of slightly collenchymatous cells devoid of chloroplasts. Leaf base (Fig. 129 C) composed of spongy tissue similar to that of the lamina and supplied by 3 widely spaced, vascular bundles. Outer part of the **scape** (Fig. 129 D) chlorenchymatous, somewhat spongy. Vascular system consisting of a circle of small, widely spaced, vascular bundles situated at the inner periphery of the chlorenchyma, and a much more deeply seated circle of 3 vascular bundles separated from the outer ring by a broad zone of collenchyma. It was impossible to decide without further investigation whether the vascular system should be interpreted as consisting of a ring of small cauline bundles surrounding a group of larger medullary ones, or whether the inner circle of larger bundles represents the main cauline system, in which case the small outer ones would be regarded as cortical.

DIONAEA (Venus's fly-trap)

Small terrestrial plants with a basal rosette of leaves whose distal ends are differentiated as traps. The latter, which consist of two lobes of the lamina united along the midrib, bear marginal cilia in the nature of emergences which interlock when the leaf is closed. Outer surface of the trap provided with **stellate trichomes** (Fig. 128 I); inner surface covered with **glands** having 2-celled stalks and multicellular heads made up of 2 tiers of cells. Glands all morphologically alike, but differentiated physiologically into deep-red digestive and colourless alluring types, the latter secreting substances which attract insects. Inner surfaces also bearing jointed, sensitive bristles which include no vascular tissue. **Mesophyll** composed of thin-walled parenchyma; palisade tissue absent. **Midrib** traversed longitudinally by a

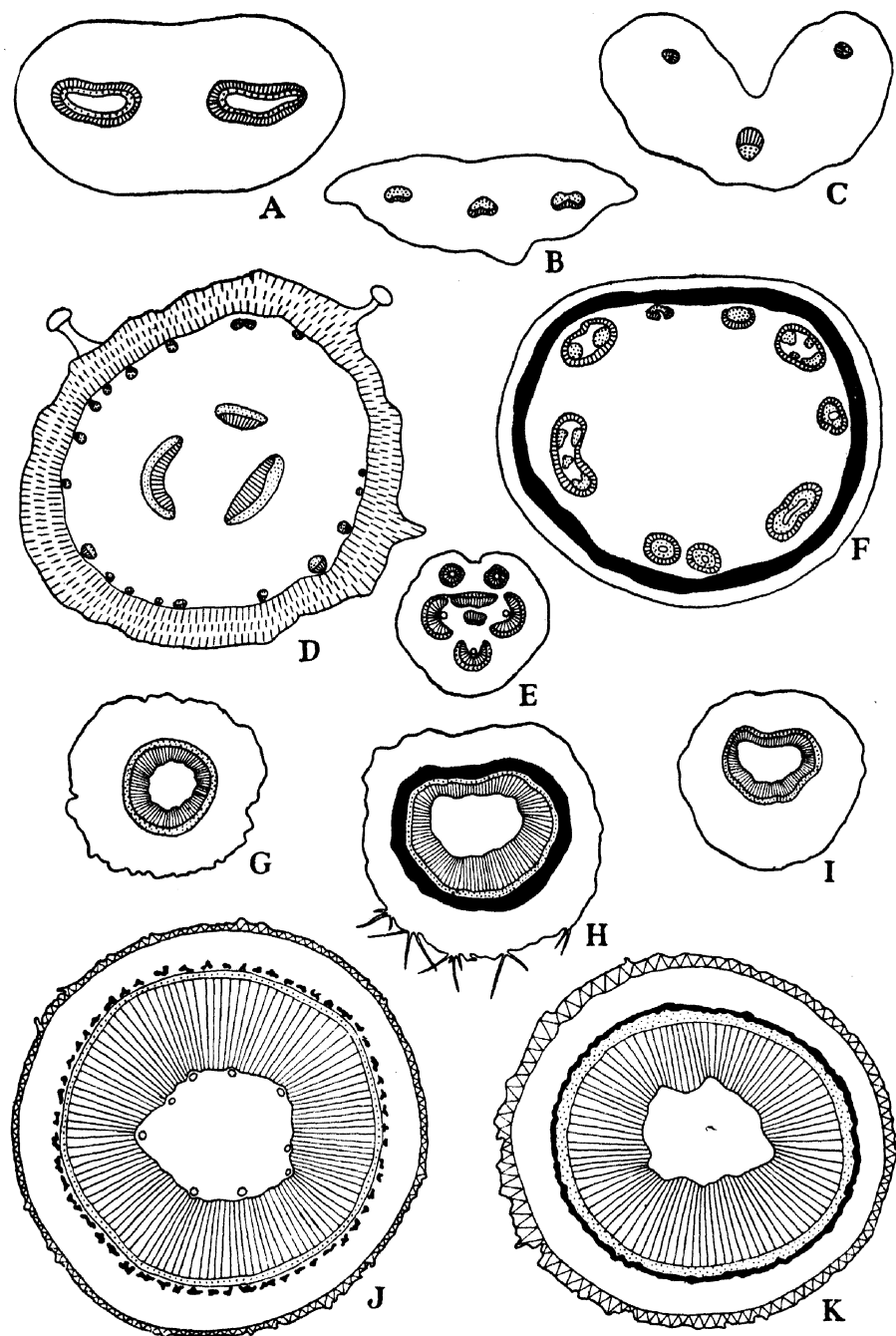


FIG. 129. DROSERACEAE, A-D and F; HAMAMELIDACEAE, E and G-K

A, *Drosophyllum binata* Labill. Petiole $\times 19$. B, *Drosophyllum rotundifolia* Linn. Petiole $\times 33$. C, *Drosophyllum lusitanicum* Link. Leaf base $\times 31$. D, *D. lusitanicum* Link. Inflorescence axis $\times 33$. E, *Liquidambar styraciflua* Linn. Petiole $\times 8$. F, *Drosophyllum binata* Labill. Inflorescence axis $\times 19$. G, *Corylopsis spicata* S. et Z. Petiole $\times 19$. H, *Fortunearia sinensis* Rehder. Petiole $\times 32$. I, *Disanthus cercidifolius* Maxim. Petiole $\times 18$. J, *Liquidambar styraciflua* Linn. Stem $\times 15$. K, *Hamamelis japonica* S. et Z. Stem $\times 15$.

double vascular bundle. Winged petiolar portion of the leaf described as having a single vascular bundle. Molisch (1547) demonstrated the presence of **tanniniferous material** in the epidermis and ground tissue of the leaf. This is normally in solution, but can be precipitated in crystalline form by treatment with hot water, dilute mineral acids, and other reagents.

ALDROVANDA

The genus is represented by a single species *A. vesiculosa* Linn., a rootless, floating plant with whorls of leaves attached to one another at their bases. Leaves somewhat resembling those of *Dionaea*, the lobed lamina with marginal bristles being differentiated as a trap at the distal end of the flattened petiole. Outer surface of the trap bearing short, 2-armed **trichomes** (Fig. 128 F), together with almost **sessile glands** with swollen, multicellular heads and a limited number of long, slender, sensitive bristles, contact with which causes the trap to close. Transverse sections of the **petiole** of *Aldrovanda* show polygonal air cavities below the epidermis, separated from one another by parenchymatous lamellae; centre of the petiole occupied by a single, somewhat reduced, vascular bundle. Vascular system of the **scape**, according to Solereder, consisting of a ring of phloem and a little xylem parenchyma, the latter enclosing an air passage.

GENERA DESCRIBED

Aldrovanda, *Dionaea*, *Drosera*,* *Drosophyllum*.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Diels 586, Lloyd 1383, Molisch 1547.

127. BYBLIDACEAE

SUMMARY

A small family of glandular herbs and small shrubs comprising the genera *Byblis* from Australia and *Roridula* from Africa. *Byblis*, which is doubtfully carnivorous, has been fully described by Lloyd (1383), who also considers that *Roridula* is not carnivorous, although it was at one time thought to be so. There are 2 species of *Byblis*, *B. linifolia* Salisb. and *B. gigantea* Lindl., both of which have rhizomes bearing the branched aerial portions of the plant with linear leaves.

BYBLIS

Leaf triangular in transverse section with rounded angles, but nearly cylindrical towards the apex; terminated by a knob with the function of a hydathode supplied by well-developed tracheidal tissue. Stalked and sessile **glands** present on all aerial parts of the plant; sessile glands on the leaf confined to longitudinal furrows with glandless ridges between them. Stalked glands scattered; provided with multicellular, umbrella-shaped heads; capable of secreting abundant mucilage. **Epidermis** composed of thick-walled cells.

Stomata situated in the furrows between the sessile glands; rubiaceous. **Mesophyll.** Portions immediately below the epidermis consisting of chlorenchyma, which is not differentiated into spongy and palisade tissue; central part occupied by colourless ground parenchyma. Vascular bundles of the leaf accompanied by mechanical tissue. In the **stem** Diels (585) records the existence of a continuous starch sheath (endodermis), bounded internally by a ring of sclerenchyma. **Vascular system** said to consist of about 9 bundles, with weakly bordered pits to the vessels in the xylem; perforations simple. Solereder describes the vascular bundles as showing transitions from the collateral to the centric type. **Pith** composed of large, lignified, pitted cells. Young **root** said to be triarch.

RORIDULA

The following information concerning the structure of *Roridula* has been taken from Solereder.

LEAF

Provided with **tentacular glands** of varying length; the latter consisting of multiseriate stalks bearing ellipsoidal heads, composed of a central group of isodiametric cells surrounded by a palisade-like secretory epidermis. Upper surface of the leaf furrowed. **Stomata** confined to the lower surface. **Mesophyll** spongy; the lower part containing large lacunae. Vascular bundles of the **veins** accompanied by sclerenchyma. In the **stem** a ring composed of fibre-like cells adjoins the vascular bundles. In *Roridula dentata* L. the wood fibres have simple pits; the isolated vessels are spirally thickened, and with bordered pitting where in contact with the rays; the perforation plates scalariform with many bars. Rays 1-2 cells wide.

TAXONOMIC NOTES

The genera *Byblis* and *Roridula* were included in the Droseraceae in the system of Bentham and Hooker. On external morphological grounds both genera have been placed by Hutchinson (1113), who followed Domin, in a separate family, the Byblidaceae, believed to be related to the Pittosporaceae. *Byblis* is also described under Byblidaceae in the Engler system, but *Roridula* in the Roridulaceae. *Byblis* was at one time also referred to the Lentibulariaceae. *Roridula* is distinguished by the scalariform perforation plates in the vessels. *Byblis*, unlike the Droseraceae, has rubiaceous stomata. The anatomical features thus tend to confirm the view that the resemblances between the 2 genera and the Droseraceae are superficial.

GENERA DESCRIBED

Byblis, *Roridula*.

LITERATURE

On General Anatomy

Diels 585, Hutchinson 1113, Lloyd 1383.

128. HAMAMELIDACEAE

(FIG. 129 on p. 584; FIG. 130 on p. 590)

SUMMARY

(i) GENERAL

A family of trees and shrubs which occur in the Far East, Madagascar, Africa, and North America. The leaf is always dorsiventral, the **hairs** almost exclusively non-glandular, and mostly tufted or stellate; **stomata**, confined to the lower surface, are rubiaceous, with one or more subsidiary cells on either side of the pore. Sclerenchymatous idioblasts of various types are common in the **mesophyll**. The vascular bundles of the **veins** are frequently surrounded by sclerenchyma, but in some species there is only an arc of sclerenchyma adjacent to the phloem. Transverse sections through the distal end of the **petiole** usually show a cylindrical or nearly closed vascular strand, accompanied, in some genera and species, by additional bundles in the wings on the adaxial side. The vascular structure of the petiole of *Liquidambar styraciflua* Linn. is more complicated. Both solitary and clustered **crystals** occur, the former sometimes appearing as transparent dots in the leaf. In the young stem the **cork** usually arises in the sub-epidermis, and the **pericycle** generally contains a composite and continuous ring of sclerenchyma. The **xylem** and **phloem**, in internodes of young stems, constitute continuous cylinders traversed by uniseriate or biseriate rays. The xylem includes numerous small, angular vessels, seldom exceeding $25\ \mu$ in diameter, and provided with scalariform perforation plates with numerous bars. Small, medullary, **secretory canals** occur in the stems of *Altingia* and *Liquidambar*, the 2 genera included in the Liquidambaroideae, and extend into the veins of the leaf as well as into the root.

(ii) WOOD

Vessels extremely small to moderately small, often entirely solitary, sometimes with a little spiral thickening, perforation plates scalariform, with few to many bars, intervascular pitting scalariform to opposite, pits to parenchyma often large and horizontally elongated; members moderately to extremely small. **Parenchyma** apotracheal, typically diffuse, but sometimes banded. **Rays** typically 2–3 cells wide, exclusively uniseriate in a few genera, heterogeneous. **Fibres** with large, distinctly bordered pits, moderately to very long. **Intercellular canals** of the traumatic type, vertical or radial, very occasionally present.

LEAF

Always dorsiventral. **Hairs** almost exclusively non-glandular, mostly tufted to stellate, often with thick walls and narrow lumina. Simple, unicellular hairs occasional. **Glandular leaf teeth**, each containing a bundle termination, composed largely of cells filled with tanniferous mucilage and provided with stomata on the upper surface, occur in *Liquidambar styraciflua* Linn. **Cork warts** reported on both surfaces in *Altingia excelsa* Nor. **Cuticle** strongly developed and granular in *Bucklandia*, *Corylopsis*, *Dicoryphe*, *Rhodoleia*, *Trichocladus*. **Epidermis** stated to include mucilaginous cells in

Rhodoleia championii Hook. f. and *R. teysmannii* Miq. **Hypoderm** on the upper side of the leaf known to occur only in *Altingia excelsa* and *A. chinensis* (Champ.) Oliver. **Stomata** confined to the lower surface; rubiaceous, with 1 or more subsidiary cells on either side of the pore. Subsidiary cells sometimes considerably elongated at right angles to the long axis of the stoma as seen in surface view. **Mesophyll** including 1 layer of palisade tissue in species of *Corylopsis*, *Disanthus*, *Fothergilla*, *Hamamelis*, *Parrotia*; 2 layers in species of *Altingia*, *Bucklandia*, *Distylium*, *Eustigma*, *Liquidambar*, *Loropetalum*, *Sycopsis*, *Trichocladus*, and several layers in *Rhodoleia*. Spongy tissue usually very lacunar. **Mesophyll** including the following types of sclerenchymatous idioblasts. (i) Branched, but short and gnarled in *Bucklandia* and *Rhodoleia*. (ii) Columnar, occasionally branched, mostly elongated in the same direction as the palisade cells in *Eustigma oblongifolium* Gard. et Champ. and *Hamamelis virginiana* L. (iii) Irregular sclerenchymatous fibres with thick walls and narrow lumina in *Dicoryphe stipulacea* J. St. Hil. (iv) Fibres similar to (iii) but with thinner walls and wider lumina in *Distylium*, *Loropetalum*, *Sycopsis*. Vascular bundles of the **veins** sheathed or accompanied by an arc of sclerenchyma in *Corylopsis*, *Dicoryphe*, *Distylium*, *Eustigma*, *Fothergilla*, *Hamamelis*, *Loropetalum*, *Parrotia*, *Sycopsis*, *Trichocladus*, i.e. in the Hamamelidoideae; sclerenchyma associated with the veins only poorly developed in *Altingia*, *Bucklandia* (sometimes lacking in this genus), *Liquidambar*, *Rhodoleia*. The bundle system of the larger leaf veins forms a ring of xylem and phloem in *Altingia* and *Liquidambar*, but is crescent-shaped in the other genera. **Petiole**, in transverse sections through the distal end, exhibiting a continuous, cylindrical vascular strand in *Corylopsis platypetala* Sieb. et Zucc., *C. spicata* Sieb. et Zucc. (Fig. 129 G), *Disanthus cercidifolius* Maxim (Fig. 129 I) (vascular ring sometimes not quite closed), *Fortunearia sinensis* Rehder (Fig. 129 H), *Fothergilla gardeni* Murr., *F. major* (Sims) Lodd., *Hamamelis mollis* Oliv., *H. virginiana* Linn., *Liquidambar formosana* Hance, *Loropetalum chinense* R. Br., *Parrotia persica* C. A. Meyer, with a very slightly interrupted cylindrical strand in *Bucklandia populnea* R. Br.; vascular strand crescent-shaped but interrupted in *Hamamelis japonica* Sieb. et Zucc. and *Sinowilsonia henryi* Hemsl.; vascular strand continuous, crescent-shaped but with the ends almost in contact with one another and somewhat prolonged towards the adaxial side in *Sycopsis sinensis* Oliv. Additional strands present in the wings in the same species of *Bucklandia* and *Liquidambar*. Vascular system, in the corresponding region of the petiole of *Liquidambar styraciflua* Linn. (Fig. 129 E), more complex, consisting of an interrupted circle of separate strands the abaxial ones of which are crescent-shaped, accompanied by 2 small cylindrical strands in the wings and an inversely orientated one in the medullary region. For further details concerning the course of the vascular bundles in a few members of the family see Morvillez (1561). **Secretory cells**, with unidentified but probably mucilaginous or tanniniferous contents, occur in the unglified tissues of the petiole in all of the above genera and species except *Sinowilsonia henryi*. **Secretory canals** present on the inside of the xylem in both species of *Liquidambar*. **Crystals** both solitary and clustered; specially large ones in the palisade tissue appear as transparent dots in species of *Corylopsis*, *Fothergilla*, *Loropetalum*, *Parrotia*, *Trichocladus*. Clustered crystals in the mesophyll

are characteristic of *Altingia*, *Bucklandia*, *Liquidambar*, *Rhodoleia*, i.e. members of the Bucklandioideae; solitary ones occur in the corresponding position in *Corylopsis*, *Dicoryphe*, *Eustigma*, *Fothergilla*, *Hamamelis*, *Loropetalum*, *Parrotia*, *Sycopsis*, *Trichocladus*, i.e. members of the Hamamelidoideae. This distinction does not hold good in the axis. Small crystals accompany the vascular bundles in *Altingia* and *Liquidambar*, but a few clustered and numerous solitary ones occur in the corresponding position in *Corylopsis* and *Hamamelis*.

AXIS

YOUNG STEM (Fig. 129 J-K)

Cork precocious in all investigated genera except in *Bucklandia* and *Rhodoleia*; originating in the sub-epidermis in *Disanthus*, *Distylium*, *Fortunearia*, *Fothergilla*, *Hamamelis*, *Liquidambar*, *Parrotia*, *Sinowilsonia*, *Sycopsis*, *Trichocladus*; composed of thin-walled cells; somewhat spongy in *Distylium*, *Parrotia*, *Sycopsis*. The development of **phelloderm** recorded or observed in *Corylopsis*, *Dicoryphe*, *Distylium*, *Hamamelis*, *Liquidambar*, *Trichocladus*. Primary **cortex**, especially the middle part, often collenchymatous; sometimes including sclerotic cells in species of *Altingia*, *Bucklandia*, *Dicoryphe*, *Distylium*, *Liquidambar*, *Sycopsis*. **Pericycle** with a composite, continuous ring of sclerenchyma in all genera except *Altingia* and *Liquidambar* (Fig. 129 J) and sometimes in *Loropetalum* where it is interrupted. Sclerenchymatous elements recorded in the secondary phloem in *Dicoryphe*, *Distylium*, *Fothergilla*, *Sycopsis*. **Xylem** and **phloem** in the internodes constituting a closed cylinder traversed by uniseriate or biseriate rays. Xylem including numerous, small, angular vessels, seldom exceeding $25\ \mu$ in diameter and provided with scalariform perforation plates with numerous bars. **Pith** usually homogeneous, but heterogeneous in *Liquidambar styraciflua* Linn. and *L. orientalis* Mill., the component cells stated sometimes to be elongated transversely to the longitudinal axis in *Altingia*, *Corylopsis*, *Hamamelis*, *Liquidambar*; longitudinally elongated in *Bucklandia* and *Rhodoleia*. **Secretory elements**. Cells, with unidentified but probably tanniniferous or mucilaginous contents, present in varying numbers in the unligified tissues of all of the species represented in the Kew slide collection except *Sinowilsonia henryi*. (For genera concerned see list of 'Genera described'.) A few (usually about 7 or 8) secretory canals occur in the pith very close to the protoxylem groups in *Altingia* and *Liquidambar*, i.e. the 2 genera in the Liquidambaroideae, each canal surrounded by small-celled epithelium, and extending into the veins of the leaf and into the root. Medullary canals recorded also in *Ostrearia*. Cortical secretory canals stated to occur in *Mytilaria* (Harms 897).

WOOD (Fig. 130)

Vessels small, varying from about 25 to $90\ \mu$ mean tangential diameter, largest (more than $50\ \mu$) in *Altingia*, *Bucklandia*, *Rhodoleia*, *Sycopsis*; Tippon (2261) gives the mean for the family as $32\ \mu$; exclusively solitary, apart from the apparent tangential pairs due to overlapping ends, in *Bucklandia*, *Distylium*, *Eustigma* (1206), *Fortunearia*, *Fothergilla*, *Hamamelis*, *Loropetalum*, *Parrotia*, *Parrotiopsis*, *Rhodoleia*, *Sycopsis*, and *Trichocladus*, with some multiples of

2 or 3 cells in the other genera; numerous, mostly 50–100 per sq. mm., but considerably more than 100 per sq. mm. in some species, e.g. *Hamamelis japonica* Sieb.; spiral thickening present in the tips of the vessel members of *Corylopsis* and *Rhodoleia* (2158) and on the walls of *Liquidambar formosana* Hance (1206); Record (1851) includes *Hamamelis* in a list of genera with

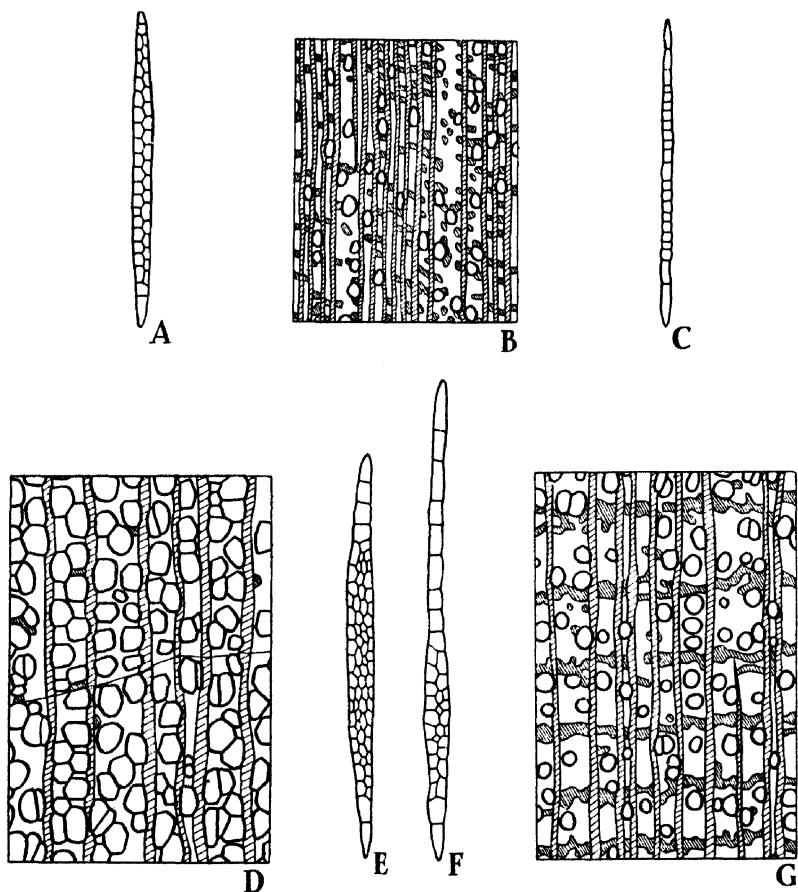


FIG. 130. HAMAMELIDACEAE

A, *Liquidambar styraciflua* Linn. B, *Trichocladus crinitus* Pers. C, *Hamamelis japonica* Sieb. et Zucc. D, *Liquidambar styraciflua* Linn. E, *Altingia excelsa* J.S.G. F, *Rhodoleia teysmanni* Miq. G, *Distylium racemosum* Sieb. et Zucc.

spiral thickening. Perforation plates all scalariform, mostly with fewer than 20 bars, but with more in *Bucklandia*, *Liquidambar*, *Rhodoleia*, and *Tetrathyrum*; the bars commonly anastomosing to give partially reticulate plates; the perforations usually without borders (2261). Intervascular pitting scalariform to opposite, difficult to find in the woods with solitary vessels; pits to ray and wood parenchyma predominantly large and horizontally elongated, simple or with distinct borders. According to Bailey, the sieve-like structures reported by Janssonius in *Altingia* are not true vested pits. Tyloses common

(2261), present, for example, in *Altingia*, *Liquidambar*, *Parrotiopsis*, and *Sycopsis*. Mean member length 0.8–2.4 mm.; longest in *Bucklandia*. **Parenchyma** apotracheal, sometimes scarce, e.g. in *Liquidambar*; typically as scattered cells (diffuse) (Fig. 130 B), but banded (metatracheal) in *Distylium* (Fig. 130 G), *Fortunearia*, *Loropetalum*, *Parrotia*, and *Sycopsis*, the bands 1 cell wide in most species but up to 3, or more rarely 4, cells wide in *Distylium*; some authors (1154, 1679) refer to paratracheal parenchyma, but it is difficult to distinguish this from diffuse parenchyma that happens to be contiguous with some of the numerous vessels. Cells commonly filled with dark gum-like substance; chambered crystal cells present in a few species. Strands of 8–16 cells. **Rays** tending to be of 2 distinct widths in a few genera, e.g. *Corylopsis*, *Eustigma*, *Sinowilsonia*, and *Tetrathyrium*; typically 2–3 cells wide, commonly up to 4 cells wide in *Altingia*; exclusively uniseriate or with only occasional small biseriate parts in *Bucklandia*, *Fothergilla*, *Hamamelis*, *Parrotiopsis* (small stem), and *Tetrathyrium*; usually less than 1 mm. high, but rather more in a few species; uniseriates in woods with multiseriate rays, numerous to only moderately numerous, usually composed of both upright and procumbent cells, but sometimes almost entirely of upright cells; typically more than 12 rays per mm. and up to 25 per mm. in *Trichocladus*, but rather fewer than 12 per mm. in *Altingia*, *Bucklandia*, *Fothergilla*, *Liquidambar*, and *Rhodoleia*; heterogeneous (Kribs's Types II A and B, and III, rarely I), typically with 4–10 marginal rows of upright cells, but seldom with more than 3 rows in *Liquidambar*, and with more than 10 rows in *Sycopsis* and *Trichocladus*. Cells usually filled with dark gummy substance; containing crystals in only a few species, e.g. *Altingia*. **Fibres** with large, distinctly bordered pits, equally numerous on both radial and tangential walls; commonly thick-walled. Tippo (2261) classifies these elements as true tracheids in the sense defined by Bailey (74). Solereder refers to spiral thickening in *Hamamelis chinensis* R. Br. Mean length 1.4–2.9 mm., longest in *Altingia* and *Bucklandia*. **Intercellular canals** of the vertical traumatic type are recorded by various authors in some species of *Altingia* and *Liquidambar* and occasional schizogenous canals are noted by Janssonius (1154) in the rays of *Altingia excelsa* Nor.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Harms (897) has drawn attention to the fact that the taxonomic subdivisions of the family exhibit corresponding anatomical differences. This applies particularly to the type of crystal in the mesophyll and to the distribution of sclerenchyma around the vascular bundles of the veins. The presence of medullary secretory canals in *Altingia* and *Liquidambar* serves to distinguish these genera from others which have been examined with the exception of *Mytilaria*.

(ii) FOR WOOD STRUCTURE

Tippo (2261). 'The secondary xylem of this family is very close in all anatomical details to certain groups in the Magnoliales as described by McLaughlin. The Magnoliales exhibit a considerable range of anatomical structures, yet it may be said that on the whole the least specialized members of that order are more primitive anatomically than are the Hamamelidaceae.'

ECONOMIC USES

Storax is the balsam produced when the bark of *Liquidambar orientalis* Mill. is wounded. It is said to be chemically distinct from the material present in the secretory canals in the same genus. It is used to a limited extent in medicine as a remedy for skin complaints. The leaves and bark of *Hamamelis virginiana* Linn. are used in medicine to prepare a cooling lotion which has astringent properties. The leaves may be recognized by the stellate or tufted hairs made up of unicellular components with thick walls and which occur particularly below the veins on the lower surface of the leaf; the rubiaceous stomata confined to the lower surface; the single layer of palisade cells; the slightly branched, sclerenchymatous idioblasts in the mesophyll; the mostly solitary crystals of calcium oxalate which occur in the mesophyll and in chambered cells which accompany the fibrous sheaths around the veins. Microscopical characters for the bark of the same species include: the cork composed of broad layers of thin-walled cells alternating with narrower zones of sclerotic cells; the zone consisting of several layers of stone cells at the inner periphery of the phelloderm; the groups of stone cells in the outer part of the secondary phloem; the groups of fibres, also in the secondary phloem, accompanied by chambered cells containing prismatic crystals; the narrow medullary rays; the absence of starch and the presence of tanniniferous substances in the parenchymatous tissues.

Various members of the family are cultivated in gardens either for their early flowers which come into bloom before the leaves develop, e.g. *Hamamelis* spp., or because of the beautiful tints assumed by the autumn foliage, e.g. *Parrotia persica* C. A. Meyer.

Useful timbers are produced by species of *Altingia* and *Bucklandia* from the Indo-Malayan region and *Liquidambar* from North America.

The American Red or Sweet Gum, *Liquidambar styraciflua* Linn., is widely used for a great variety of purposes, but particularly for furniture and interior trim.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Altingia, *Bucklandia*,* *Corylopsis*,* *Dicoryphe*, *Disanthus*,* *Distylium*,* *Eustigma*, *Fortunearia*,* *Fothergilla*,* *Hamamelis*,* *Liquidambar*,* *Loropetalum*,* *Maingaya*, *Mytilaria*, *Ostrearia*, *Parrotia*,* *Rhodoleia*, *Sinowilsonia*,* *Sycopsis*,* *Trichocladus*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Altingia, *Bucklandia*, *Corylopsis*, *Disanthus*, *Distylium*, *Eustigma*, *Fortunearia*, *Fothergilla*, *Hamamelis*, *Liquidambar*, *Loropetalum*, *Parrotia*, *Parrotiopsis*, *Rhodoleia*, *Sinowilsonia*, *Sycopsis*, *Tetrathyrium*, *Trichocladus*.

LITERATURE

(i) *On General Anatomy*

Harms 897, Holm 1024, Morvillez 1561, Puri 1763, Starr 2188, Varossieau 2324.

(ii) *On Wood Structure*

Bailey 74, Beekman 167, den Berger 179, 182, den Berger and Endert 183, Brown and Panshin 288, 289, Chowdhury 411, Desch 574, Greguss 2522, Hale 870, Howard 1088, Janssonius 1154, Jones 1191, Kanehira 1206, 1209, Lecomte 1334, Nicoloff 1593, Pearson and Brown 1679, Record 1780, 1783, 1787, 1800, 1801, 1818, 1825, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2203, Sudworth and Mell 2217, Tang 2231, Tippo 2261, Webber 2377, Varossieau 2324.

129. MYROTHAMNACEAE

SUMMARY

(i) GENERAL

A small family of xeromorphic, resinous shrubs, consisting of 2 species of the single genus *Myrothamnus* from Africa and Madagascar. Important anatomical characters include the occurrence of **resin cells** in the epidermis of the leaf and of ranunculaceous **stomata**, whilst in the **xylem** of the axis the small angular vessels mostly have scalariform perforation plates with many bars.

(ii) WOOD

Vessels small, mostly solitary, perforation plates scalariform, members moderately long. **Parenchyma** absent. **Rays** uniseriate and heterogeneous. **Fibres** with bordered pits.

LEAF

Hairs absent. **Cuticle** fairly thick, but thinner above the resin cells of the epidermis. **Epidermis** mostly composed of polygonal cells, but including scattered, enlarged, resin cells. **Stomata** ranunculaceous. **Mesophyll** isobilateral, consisting of tangentially elongated cells towards the centre, but composed of palisade cells elsewhere. Vascular bundles of the **veins** embedded in the mesophyll. Cluster **crystals** present.

AXIS

YOUNG STEM

Xylem cruciform when young but later forming a continuous cylinder; including, according to Solereder, small, quadrangular vessels with minute bordered pits and perforation plates which are very oblique, with many bars, or consist of small elliptical pits arranged in parallel rows; thick-walled fibres with inconspicuously bordered pits; uniseriate rays. **Pith** composed of cells elongated in the same direction as the axis.

WOOD¹

Vessels very small (mean diameter about 35 μ); mostly solitary, but with some groups; perforation plates scalariform with about 45 bars and very oblique; intervacular pitting transitional and opposite; pits to ray cells similar. Mean member length about 0.9 mm. **Parenchyma** absent. **Rays** exclusively uniseriate, heterogeneous (Kribs's Type III). **Fibres** with bordered pits.

¹ Based entirely on the description given by Tippo (2261).

TAXONOMIC NOTES

Myrothamnus was included in the Hamamelidaceae in the Bentham and Hooker system. While it is still generally held that the genus is related to the Hamamelidaceae, Hutchinson (1113) and Niedenzu and Engler (1599) treat it as a distinct family. The presence of resin cells in the leaf epidermis and of ranunculaceous stomata are anatomical characters which favour the separation of the Myrothamnaceae from the Hamamelidaceae. Tippo (2261) has pointed out that the wood structure in the 2 families is very similar.

GENUS DESCRIBED

Myrothamnus.

LITERATURE

(i) *On General Anatomy*

Hutchinson 1113, Niedenzu and Engler 1599, Zemke 2505.

(ii) *On Wood Structure*

Record 1843, 1851, Thompson 2254, Tippo 2261.

130. BRUNIACEAE

(FIG. 131 on p. 598)

SUMMARY

Heath-like shrubs from South Africa. In correlation with the habit, the leaf is often centric, but tends to be partly or wholly dorsiventral in some species. The apex of the mature leaf, except in *Audouinia*, usually bears a small projection composed of suberized cells. In species with strongly adpressed leaves the palisade tissue is sometimes confined to the lower surface. The distribution of the **stomata**, which are ranunculaceous but surrounded by rather small epidermal cells, also varies somewhat according to the morphology of the leaves and the extent to which they overlap or are adpressed to the stem. The **hairs** are mostly long, slender and unicellular, with thick smooth walls and narrow lumina. The narrow primary **cortex** of the **stem** sometimes contains stone cells, whilst the **xylem** is characterized by small vessels having scalariform perforation plates with numerous bars, and fibres with bordered pits. **Crystals** both solitary and clustered.

LEAF

Usually centric, but sometimes dorsiventral or intermediate between the 2 types. **Hairs** mostly long, slender, unicellular with a thick smooth wall and narrow lumen; sometimes accompanied by shorter hairs in *Audouinia*. The tip of the leaf, except in *Audouinia*, consists of a cap of cork cells replaced, as the outermost ones become detached, by the activity of a central meristem. **Cuticle** thick, especially on the outwardly directed abaxial surface; smooth but longitudinally striate in *Berzelia lanuginosa* (L.) Brongn., and *Nebelia paleacea* (Berg.) O. Kze. Cells of the **epidermis** large, especially above and below the median vein, progressively smaller towards the margin; more or less arched outwards; sometimes papillose. Distribution of **stomata** varying according to the external morphology of the leaf, several distinct types occur-

ring within some of the genera; confined to the lower surface in *Linconia cuspidata* (Thunb.) Swartz and *Pseudobaeckea*; restricted to the upper side in species with broad scaly leaves belonging to the genera *Brunia*, *Lonchostoma*, *Pseudobaeckea*, and *Raspalia*; frequently arranged in 1-5 longitudinal rows with the long axis parallel to the median vein, but exceptions occur. The 4-7 surrounding cells are often rather smaller than those of the remainder of the epidermis. **Mesophyll.** Palisade tissue consisting of 1, or occasionally 2, layers; confined to the abaxial surface in species with adpressed leaves. Sclerenchymatous cells recorded by Solereder in the mesophyll of *Linconia cuspidata* and observed in *Lonchostoma monostylis* Sond. **Water-storage cells** reported to occur at the apex of the leaf near the terminations of the veins. Leaf often traversed by 3 **veins**, but 5 or even as many as 20 recorded in certain species. **Crystals** usually present, except in *Raspalia*, in the mesophyll or around the vascular bundles; more frequently clustered than solitary. Mesophyll cells observed to have apparently tanniniferous contents in *Lonchostoma monostylis*.

AXIS

STEM (Fig. 131 G)

Cells of the **epidermis** arched outwards. **Cork** thin-walled, arising immediately below the epidermis. Primary **cortex** narrow; containing sclerod cells in species of *Brunia*, *Nebelia*, *Staavia*, *Tittmannia*. **Pericycle** usually containing a composite ring of sclerenchyma. **Xylem**, according to Niedenzu and Harms (1600), characterized by small, mostly isolated vessels having scalariform perforation plates with many bars (this was confirmed by direct observation for *Audouinia capitata* (Thunb.) Brogn., but many of the vessels in *Lonchostoma monostylis* Sond. were seen to be in tangential pairs, frequently arranged to form irregular clusters); fibres with bordered pits; scanty parenchyma; rays 1-3 cells wide with, according to Solereder, the distal ends enlarged where traversing the phloem. **Pith** in *Audouinia capitata* and *Lonchostoma monostylis* seen to be composed of somewhat elongated, fairly thick-walled, pitted cells. **Resinous deposits** observed in *Audouinia capitata* situated in certain of the cells of the cork, phloem, medullary rays, and pith, those in the phloem being elongated and resembling narrow sacs. Similar deposits much less numerous or almost absent in *Lonchostoma monostylis*.

GENERA DESCRIBED

Audouinia,* *Berzelia*, *Brunia*, *Linconia*, *Lonchostoma*,* *Nebelia*, *Pseudobaeckea*, *Raspalia*, *Staavia*, *Tittmannia*.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Niedenzu and Harms 1600.

131. HALORAGACEAE

(FIG. 131 on p. 598; FIG. 132 on p. 600)

SUMMARY

Herbs, often very large, which grow in or near water in many parts of the world. The plants are frequently covered with a variety of **hairs**, **warts**, and **emergences**, some of the hairs being glandular. Some of the glandular structures on the stem of *Gunnera* serve as channels for the ingress of colonies of the blue-green alga *Nostoc*, which are normally to be found in the superficial layers of the stem. The **stomata** are usually ranunculaceous, and are said sometimes to be ephemeral. The **mesophyll** is dorsiventral or sub-centric, but typical palisade cells are seldom differentiated. Clustered **crystals** are common. The vascular system of the **petiole** of *Gunnera* consists of separate steles. The primary **cortex** of the stem contains numerous air-cavities, which are particularly well developed in aquatic species. The **vascular system** of the stem exhibits varying degrees of complexity, culminating in the polystelic network which occurs particularly in the upper internodes of *Gunnera*. Each stele is surrounded by a well-defined endodermis with Casparian thickenings. In the **xylem** the relatively narrow vessels with simple perforations are embedded in ground tissue consisting of fibres with thick walls, narrow lumina, and simple pits. Batham (151) has shown that the cauline vascular structure of the relatively small species of *Gunnera* which occur in New Zealand is similar to, although less complex than that of, the large species from other countries. The vascular system of the New Zealand species is said to consist of a tube with leaf trace gaps in the sides. To quote Batham's words: 'The "polystelic" state suggested by isolated sections resolves itself, when surveyed three dimensionally, into a hollow monostele with foliar gaps and branches.'

LEAF

Dorsiventral or sub-centric. **Hairs**. (i) Unicellular in species of *Gunnera* and *Haloragis*. (ii) Uniseriate in *Haloragis*, *Laurembergia*, *Loudonia*, *Meziella*, *Myriophyllum*, *Proserpinaca*. (iii) Glandular, sometimes flask-shaped, shaggy types appear under the lens as small dots, in the leaf teeth, &c.; composed of polygonal cells containing highly refractive oily bodies in all genera except *Loudonia*. Hemispherical warts (colleters), with the epidermal cells arranged in the form of a fan as seen in longitudinal section, recorded in several species of *Gunnera* (Fig. 132 F). Other types of hairs and wart-like structures also occur in the family. For further particulars of hairs and related structures in *Gunnera macrophylla* Bl. see Skottsberg's (2121) article. **Stomata** usually ranunculaceous, more numerous in species with aerial than in those with submerged leaves; stated sometimes to be ephemeral; usually present on both surfaces of the leaf; smaller and less numerous on the upper than on the lower surface in terrestrial species of *Haloragis* and *Loudonia*. **Mesophyll** frequently devoid of palisade cells, but these sometimes occur in *Haloragis* and *Loudonia*. **Petiole**. Larger vascular strands of *Gunnera* consisting of distinct steles, frequently composed of central xylem surrounded by an

endodermis, but in certain species including a sclerenchymatous pith or pseudopith. The pith, in the most complex types of all, is replaced by a vascular system consisting of central strands of phloem enclosing some xylem vessels, the whole being surrounded by 2 collenchymatous sheaths and supported by 2 strands of fibres. Transverse sections through the distal end of the petiole of *Haloragis alata* Jacq. (Fig. 131 F) exhibit an arc of widely spaced vascular bundles, each surrounded by a distinct endodermis. Tannin common. **Crystals** clustered; usually small, but large ones occurring in *Gunnera*.

AXIS

STEM (Fig. 131 E)

Glands resembling shaggy hairs, with only narrow canals between them, but covered with a cap-shaped layer of epidermal cells (Fig. 132 G), occur between the leaf bases in *Gunnera macrophylla* Bl. The glands secrete mucilage containing tannin, which swells up and ruptures the cap of epidermal cells. They sometimes serve as an entrance for colonies of the blue-green alga *Nostoc* which become established in the outer part of the stem. An account of a developmental study of the symbiotic relationship between *Nostoc* and *Gunnera* has been published by Miehe (1516). Primary **cortex** containing numerous air cavities, those in aquatic being much larger than the ones in terrestrial species. Air cavities radially elongated and arranged in a ring in *Myriophyllum* and *Serpicula* (Fig. 132 A). Cortex said to contain palisade tissue and small strands of fibres in the sub-epidermal region of *Loudonia*; outer part seen to consist of spongy assimilatory tissue in *Haloragis alata*. **Endodermis**, especially in aquatic species, more or less well defined. Isolated groups of sclerenchymatous cells recorded in the **pericycle** of a few species of *Haloragis*, *Loudonia*, *Proserpinaca*. **Vascular system** exhibiting various degrees of complexity in different genera and species. (a) Consisting of an axile, fibro-vascular mass without true pith in *Myriophyllum*. A pseudopith is formed in older stems of this genus by resorption of the central primary vessels. (b) Structure more or less normal with a ring of cambium and a continuous cylinder of secondary xylem traversed by narrow rays in terrestrial species such as *Haloragis alata* (Fig. 131 E) and *Loudonia aurea* Lindl. (c) With a large or small number of variously orientated, separate steles in *Gunnera*, particularly in the higher internodes. Each stele is surrounded by a well-defined endodermis with Casparian thickenings on the radial walls, followed on the inside by a pericycle of 1 or 2 cells broad, 2-6 isolated strands of phloem, and finally the central xylem consisting of vessels embedded in thin-walled parenchyma. For details concerning the relatively simple but polystelic structure of the small species of *Gunnera* from New Zealand see Batham (151). **Xylem** including vessels with narrow lumina, simple perforations, and, where in contact with the rays, bordered pits. Wood fibres composed of elements with fairly thick walls, narrow lumina, and simple pits. The above remarks concerning the xylem refer particularly to *Haloragis*, but simple perforations in the vessels are stated to occur throughout the family. **Pith** frequently absent, but fairly broad and consisting of somewhat spongy parenchyma in *Haloragis alata*. **Crystals**, situated in hair-like cells, recorded in the cortex of species of *Haloragis*, *Laurembergia*, *Meziella*, *Myriophyllum*,

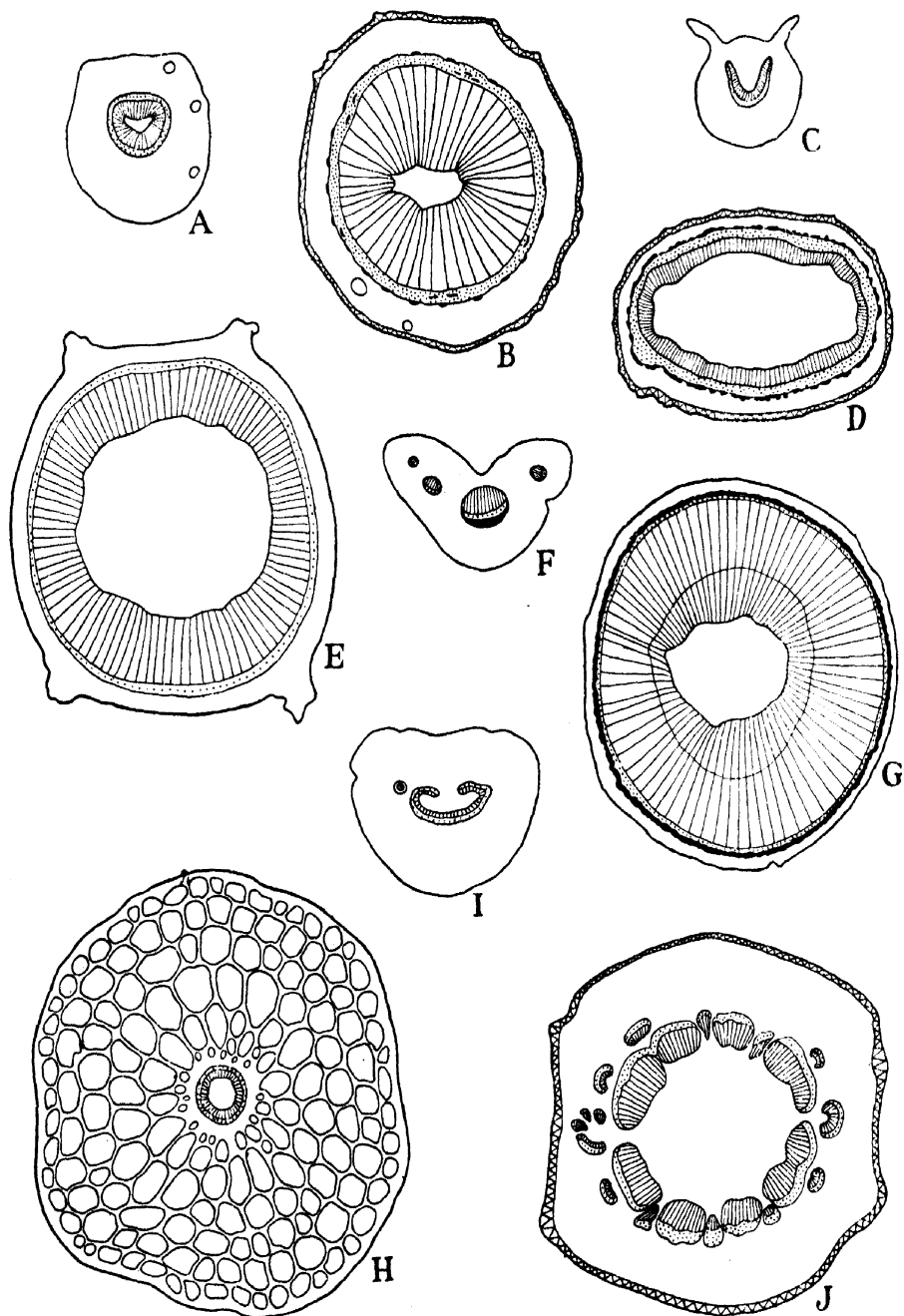


FIG. 131. COMBRETACEAE, A-D; HALORAGACEAE, E-F; BRUNIACEAE, G; HIPPURIDACEAE, H; RHIZOPHORACEAE, I-J

A, *Terminalia chebula* Retz. Petiole $\times 8$. B, *T. chebula* Retz. Stem $\times 13$. C, *Calycotris floribunda* Lam. Petiole $\times 8$. D, *C. floribunda* Lam. Stem $\times 8$. E, *Haloragis alata* Jacq. Stem $\times 15$. F, *H. alata* Jacq. Petiole $\times 15$. G, *Lonchostoma monostylis* Sond. Stem $\times 15$. H, *Hippuris vulgaris* Linn. Stem $\times 8$. I, *Bruguiera gymnorhiza* Lam. Petiole $\times 8$. J, *B. gymnorhiza* Lam. Stem $\times 6$.

Proserpinaca, *Serpicula*. Solitary and clustered crystals observed in the pith of *Haloragis alata*. Acicular crystals recorded in 1 species of *Gunnera*.

STOLON

Stolons of *Gunnera* exhibit 2 rings of xylem and phloem, the inner one being inversely orientated. One or more steles present in different species. For particulars of the vascular structure of the stolons of New Zealand species of *Gunnera* see Batham (151).

ROOT

Roots of New Zealand species of *Gunnera* said by Batham (151) probably to consist entirely of primary xylem and phloem.

ECONOMIC USES

The large species of *Gunnera* are frequently cultivated in marshy places in big gardens on account of their striking foliage.

GENERA DESCRIBED

Gunnera, *Haloragis*,* *Laurembergia*, *Loudonia*, *Meziella*, *Myriophyllum*, *Proserpinaca*, *Serpicula*.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Batham 151, Mische 1516, Skottsberg 2121.

132. CALLITRICHACEAE

Cosmopolitan, terrestrial or aquatic, annual or perennial herbs belonging to the single genus *Callitriche*. The **hairs** of terrestrial species include glands each having a foot and an 8-celled head covered with a vesicular cuticle. Stellate hairs recorded in the section *Eucallitriche*. **Stomata** numerous on both surfaces of the leaf and on the stem in terrestrial species; absent from the stem, but occurring sporadically on the leaves in submerged forms; confined to the upper surface of floating leaves; sometimes ephemeral in submerged species. **Vascular system** of the stem reduced to a weak, axile bundle. **Pith** consisting of only 2 or 3 cells.

GENUS DESCRIBED

Callitriche.

LITERATURE

On General Anatomy

Pax and Hoffmann 1674.

133. HIPPURIDACEAE

(FIG. 131 on p. 598; FIG. 132 on p. 600)

SUMMARY

A family represented by the aquatic herb *Hippuris vulgaris* Linn. which occurs in many North Temperate regions.

LEAF

Leaves isobilateral to centric. Peltate **hairs** (Fig. 132 B-D) each with a unicellular foot and multicellular head present. **Stomata** occur on both surfaces. Outer part of the **mesophyll** towards both surfaces and at the

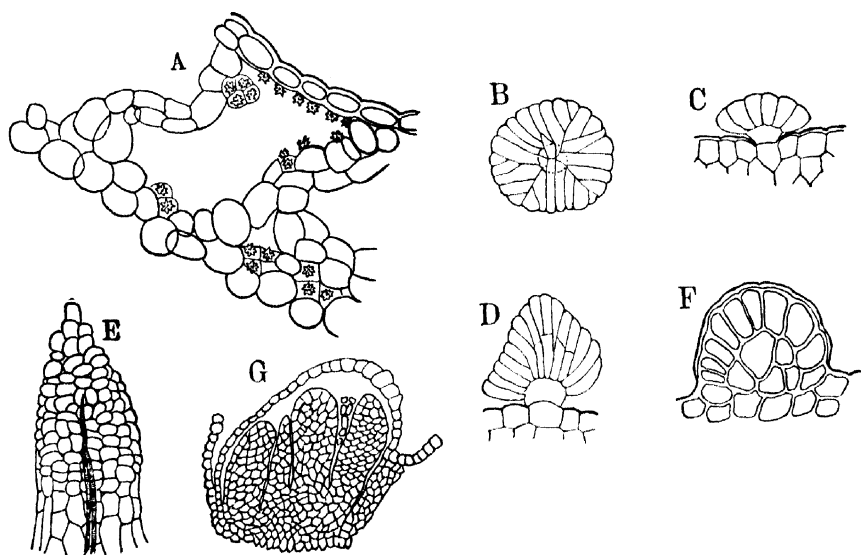


FIG. 132. HALORAGACEAE, A and E-G; HIPPURIDACEAE, B-D

A, Transverse section through a piece of the cortex of *Serpicula repens*, L. B-D, Peltate hairs of *Hippuris vulgaris* L.; B in surface-view, C in section; D, fan-shaped peltate hair. E, Tip of a segment of the leaf of *Myriophyllum verticillatum* L. F, Colleter from the leaf of *Gunnera macrophylla* Bl. G, Longitudinal section through a stem-gland of *Gunnera macrophylla*.—A and E by Solereder, B-D after Rauter, F and G after Merker.

margins composed of a single layer of somewhat palisade-like cells, interspersed by numerous air cavities, the latter being especially well developed below the stomata. Palisade tissue not very clearly differentiated from the spongy parenchyma at the centre of the mesophyll. **Vascular bundles** poorly developed, embedded in the mesophyll, and surrounded by a single-layered sheath of parenchymatous cells.

AXIS (Fig. 131 H)

The axis consists of a rhizome bearing erect branches. The following particulars refer to the latter.

Outer and inner tangential walls of the cells of the **epidermis** considerably thickened, the radial ones less so. Primary **cortex** broad, the whole of it,

except for 2 sub-epidermal layers of cells, permeated by large intercellular spaces elongated in the same direction as the axis, the cavities being separated from one another by multicellular plates only 1 cell wide. Intercellular spaces also interrupted at the nodes by transverse plates of small-celled tissue containing the leaf traces. **Endodermis** well defined; for details of its development see Barratt (142). **Vascular system** reduced to an axile strand of thin-walled tissue, the outer part consisting of a narrow zone of phloem and the inner part of a broader region of xylem. Vessels small in diameter, with spiral or reticulate thickening. According to Solereder a pseudo-pith is formed in old stems from the central primary vessels.

TAXONOMIC NOTES

Hippuris is sometimes treated as a member of the Haloragaceae, but in the Engler and Prantl system is given the status of a separate family. The anatomical structure of the plant is that of a hygrophyte, and provides little information concerning the taxonomic affinities of the plant. The conspicuous endodermis and the axile vascular system are not unlike those of the less complex members of the Haloragaceae such as *Myriophyllum*.

GENUS DESCRIBED

Hippuris.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Barratt 142.

134. RHIZOPHORACEAE

(FIG. 131 on p. 598; FIG. 133 on p. 604; FIG. 134 on p. 606; FIG. 135 on p. 608)

SUMMARY

(i) GENERAL

Trees and shrubs, some of which constitute the chief component of the mangrove swamps around tropical shores and estuaries. The mangrove plants belonging to this family are characterized by **stilt-roots**, only the lower parts of which are subterranean. The **cortex** of these stilt roots is sponge-like in structure owing to the development of a complex intercellular system. The leaf is usually dorsiventral, but tends to be centric in some species. The **hairs** are mostly unicellular. The **cuticle** is often very thick. The **epidermis** frequently consists of more than 1 layer, but a true **hypoderm** is also common. **Stomata** in the leaf, confined to the lower surface, are frequently depressed and provided with a well-developed front cavity, which is sometimes divided into 2 distinct parts. Subsidiary cells are not usually differentiated from those of the remainder of the epidermis, although the epidermal cells around the stomata are sometimes more oblong than their neighbours. **Sclerenchymatous idioblasts** occur in the mesophyll of the leaf, in the cortex and pith of the stem of *Bruguiera* and *Rhizophora*, as well as in the stilt roots. The **cork** in young stems generally arises superficially,

and the **xylem**, in some genera, is traversed by fairly broad primary medullary rays. Cells containing **tannin** are frequent in all tissues.

(ii) WOOD

GROUP I. Rhizophoreae (*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*)

Vessels moderately small, with fairly numerous and sometimes long multiples and clusters; perforation plates exclusively scalariform with few and thick bars; intervacular pitting scalariform; members of medium length to moderately long. **Parenchyma** typically scanty paratracheal; banded in *Kandelia*. **Rays** mostly 3–6 cells wide, often more than 2 mm. high, uniseriate rays rare, homogeneous or heterogeneous, with the procumbent cells almost square. **Fibres** with small simple pits, of medium length.

GROUP II. Gynotrocheae (*Anisophyllea*, *Carallia*, *Combretocarpus*, *Crossostylis*, and *Gynotroches*)

Vessels medium-sized to large and often very few; perforation plates simple, intervacular pitting typically alternate; pits to parenchyma commonly elongated and unilaterally compound. Members of medium length to moderately long. **Parenchyma** typically banded or aliform, the bands varying from narrow to broad and from regular and metatracheal to irregular and confluent, often with some diffuse cells. **Rays** up to 10–15 cells wide and very high, uniseriate rays numerous, markedly heterogeneous. **Fibres** with bordered pits, moderately to very long.

GROUP III. Macarisieae (*Anopyxis*, *Blepharistemma*, *Cassipourea*, *Macarisia*, and *Sterigma petalum*)

Vessels small to large, often exclusively solitary; perforation plates simple and scalariform (with fine bars), intervacular pitting opposite to alternate; pits to parenchyma mostly elongated, tending to be horizontal to wood parenchyma and irregular to ray cells; members moderately to very long. **Parenchyma** typically predominantly paratracheal and limited to the abaxial sides of the vessels, varying from aliform to confluent, with some diffuse; in predominantly apotracheal bands in some genera. **Rays** mostly 3–4 cells wide and less than 1 mm. high, uniseriate rays numerous, markedly heterogeneous. **Fibres** with large and distinctly bordered pits, moderately long.

LEAF (Fig. 133 A)

Usually dorsiventral; tending to be centric in species of *Anisophyllea*, *Ceriops*, *Kandelia*. **Hairs** mostly unicellular with thick or thin walls; tufted trichomes recorded in *Macarisia*. Glandular shaggy hairs, present on the inside of the stipules in certain species, sometimes secrete a gum-like substance on the vegetative buds. **Cork warts** occur as small black spots on the lower side of the leaf of species of *Carallia*, *Rhizophora*, *Weihea*. Similar structures, described as glands and said to be formed by resorption of the cells of the epidermis and hypoderm, recorded by Engler (633) in *Poga oleosa* Pierre. **Cuticle** often very thick; described by Arzt (45) as consisting of 2 chemically distinct layers in mangroves, the thicker outer layer staining yellow and the inner an intense brown when treated with chlor-zinc-iodide. A

single-layered **epidermis** on the upper surface recorded only in a few species of *Blepharistemma*, *Carallia*, *Weihea*; locally 2-layered in several species of *Cassipourea*. **Hypoderm** towards the upper surface 1-layered in various species of *Bruguiera*, *Crossostylis*, *Gynotroches*, *Macarisia*; 1- or 2-layered in *Anapxyis*; 2- or more-layered in species of *Ceriops*, *Poga oleosa*, and *Rhizophora*, the innermost layer in *Poga oleosa* including, according to Engler (633), large, solitary, mucilage cells. According to Bowman (251) the number of layers of hypoderm cells in *Rhizophora mangle* Linn. is controlled by the concentration of salt in the water in which the plants are growing, high salt concentration being associated with an increased number of hypodermal layers. The leaves are also thicker when grown in normal than in diluted sea water because the tanniferous cells (see below) are larger. A 2-layered epidermis accompanied by a layer of hypoderm is stated to occur in *Dactylopetalum* and *Kandelia*. A single-layered hypoderm towards the lower surface also recorded by Mullan (1570) in *Ceriops candolleana* Arn. and in *Poga oleosa* by Engler (633). Cells of the epidermis, hypoderm, and mesophyll sometimes mucilaginous, e.g. in species of *Blepharistemma*, *Carallia*, *Dactylopetalum*, *Gynotroches*, *Rhizophora*. **Stomata** confined to the lower surface; depressed and often provided with a front cavity, the latter sometimes divided into 2 distinct parts; surrounding cells sometimes more oblong than those of the remainder of the epidermis in *Blepharistemma*, *Bruguiera*, *Ceriops*, *Kandelia*. A mixture of ranunculaceous, cruciferous, and rubiaceous stomata recorded by Sprague and Boodle (2173) in *Anapxyis ealaensis* Sprague. **Mesophyll**. Palisade tissue consisting of 1-4 layers in different genera and species. Spongy tissue usually with large intercellular spaces; very dense in *Weihea zeylanica* Baill.; collenchymatous in *Bruguiera gymnorhiza* Lam.; sometimes containing aqueous cells in *Bruguiera* and *Kandelia*. H-shaped sclerenchymatous idioblasts (Fig. 133) occur in the palisade tissue, and variously branched ones in the spongy mesophyll of *Rhizophora*. Solitary sclerenchymatous cells also recorded by Engler (633) in the spongy mesophyll of *Poga oleosa*. Vascular bundles of the **veins** mostly embedded in the mesophyll; almost vertically transcurrent in a species of *Macarisia*; rarely accompanied by well-developed sclerenchyma except in a species of *Gynotroches*; sclerenchyma above and below the smaller veins recorded by Sprague and Boodle (2173) in *Anapxyis*; surrounded by starch sheaths in *Ceriops candolleana* Arn. according to Mullan (1570). Enlarged terminal tracheids reported in *Bruguiera*, *Ceriops*, *Kandelia*. **Petiole**, in transverse sections through the distal end, exhibiting: a crescent-shaped strand in *Anapxyis* according to Sprague and Boodle (2173); structure similar in *Bruguiera gymnorhiza* Lam. (Fig. 131 1); exhibiting a ring of bundles surrounding additional medullary strands in *Rhizophora mucronata* Lam.; similar but with a single medullary bundle in *Ceriops candolleana* according to Mullan (1570). **Crystals** mostly clustered in *Bruguiera*, *Carallia* (in the epidermis), *Ceriops*, *Gynotroches*, *Kandelia*, *Rhizophora*; mostly solitary in *Anapxyis* (occasional in the epidermis), *Blepharistemma*, *Cassipourea*, *Macarisia*, *Weihea* (particularly in the epidermis). **Secretory elements**. Cells containing tannin recorded in the mesophyll of *Anapxyis*, *Ceriops* (cells elongated), *Rhizophora*, and probably present in other genera and species as well. Secretory canals with brownish contents occur in the spongy mesophyll of *Poga oleosa* according

to Engler (633). Large globules of oil said to be present in the cells surrounding the stomata and in the palisade cells of *Bruguiera*.

Axis

YOUNG STEM (Fig. 131 J and 133 B)

Epidermis of *Bruguiera caryophylloides* Blume composed of variously shaped cells appearing conical in transverse sections; including vertically divided cells in *Ceriops*. Stem of *Bruguiera caryophylloides* grooved when sufficiently young. **Cork** arising superficially, usually in the hypodermis, in

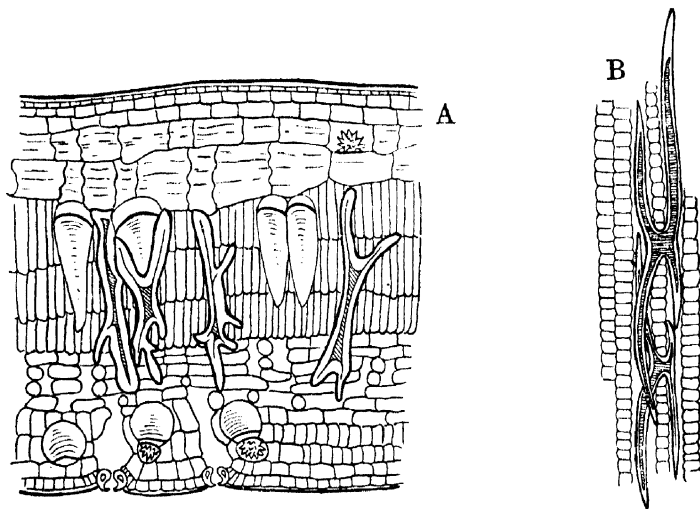


FIG. 133. RHIZOPHORACEAE

A, Transverse section of the leaf of '*Rhizophora conjugata* L.'. B, H-shaped idioblasts from the cortex of the branch of *Rhizophora mangle* L.—A, by Solereder, B, after Warming.

species of *Anapaxis*, *Bruguiera*, *Carallia*, *Ceriops*, *Rhizophora*; spongy in *Ceriops* and *Rhizophora mangle* Linn.; component cells provided with thickened inner walls in *Anapaxis*. Primary **cortex** lacunar in species of *Bruguiera*, *Ceriops*, and *Rhizophora*; outer part containing strongly lignified stone cells in *Bruguiera caryophylloides*; including H-shaped sclerenchymatous idioblasts in *Rhizophora mangle* (present in the pith as well in this genus); occasional sclerotic cells recorded by Sprague and Boodle (2173) in *Anapaxis*. **Pericycle** with a sub-continuous, composite ring of sclerenchyma in *Anapaxis*; described as including very small fibres in *Rhizophora mucronata* Lam. and isolated strands of fibres in *Bruguiera caryophylloides* and *Ceriops candolleana* Arn. according to Mullan (1570). No pericyclic fibres observed in young stems of *Bruguiera gymnorhiza* Lam. (Fig. 131 J). **Xylem** traversed by rays 2–3 cells wide in *Rhizophora mucronata* and by rays 5–6 cells wide in *Ceriops candolleana*. Vessels with scalariform perforation plates. **Crystals** of the same types as those in the leaf; crystalliferous cells recorded in the pericycle of *Ceriops*. **Secretory elements**. Vertically elongated secretory cells containing tannin and/or oil present in the cortex and pith of *Ceriops*; similar elements probably occur in other genera as well.

BARK

Secretory cavities, originating from groups of cells which become mucilaginous, recorded by Engler (633) in *Poga oleosa* Pierre. For anatomy of the tanniferous barks of *Rhizophora*, &c., see 'Economic Uses' on p. 611.

WOOD

The genera have been divided into 4 groups, as proposed by Marco (1439).

GROUP I. *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* (Fig. 134 A-C)

Vessels moderately small (50–100 μ mean tangential diameter), solitary and in radial multiples often of more than 4 cells and up to 14, and in clusters; mostly 5–35 per sq. mm. (Panshin (1649) gives 25–70 for *Ceriops*). Perforation plates scalariform, steeply inclined, and with rather thick and few bars. Intervascular pitting scalariform, the pits narrow, crowded, and extending completely across the member wall. Pits to ray cells differing from those to the wood parenchyma; the former typically small and round to oval, 2 to several such pits fitting a single large, vertical or obliquely elongated pit in the ray cell wall; the ray pit very broad and shield-shaped in *Ceriops* and often subtending more than 1 row of vertical vessel pits; pit-pairs between vessels and wood parenchyma typically oval or elongated in both walls, the longer axes of the pits horizontal. Tyloses often present, sometimes abundant. Mean member length 0.6–1.0 mm. **Parenchyma** paratracheal, scanty except in *Kandelia*; and often consisting of only a few cells touching the vessels (Fig. 134 A); more abundant in *Kandelia*, forming complete sheaths round the vessels and in bands 2–4 cells wide linking up the vessels (Fig. 134 C). Strands of 4–8 cells. **Rays** mostly up to 3–6 cells wide, sometimes up to 10 cells in *Bruguiera* and *Rhizophora* (1439); seldom more than 3 mm. high in *Ceriops* and *Kandelia*, often more than 3 mm. in *Bruguiera* and *Rhizophora*; uniseriate rays typically scarce to almost absent, except in *Ceriops* in which they are moderately abundant and composed of both upright and procumbent cells; 6–10 rays per mm.; heterogeneous (Kribs's Type II A?) except in *Rhizophora*, with 3 or 4 marginal rows of upright cells and up to 10 rows in *Ceriops*, the inner 'procumbent' cells short radially and almost square; uniseriate rays similar. In *Rhizophora* the rays are homogeneous (Kribs's Type II) and composed mainly of definitely procumbent cells and in *Bruguiera* almost homogeneous. Cells commonly containing dark gummy contents and single crystals; containing silica in *Kandelia candel* Druce (794). **Fibres** with small simple pits and thick walls, the walls often gelatinous (1439). Some septate fibres observed in a specimen of *Kandelia Rheedii* W. et A. Mean length 1.1–1.7 mm.

GROUP II. *Anisophyllea*, *Carallia*, *Combretocarpus*, *Crossostylis*, and *Gynotroches* (Fig. 134 D-F)

Vessels medium-sized (100–200 μ mean tangential diameter) in *Crossostylis* and *Gynotroches*, large (more than 200 μ) in *Anisophyllea*, *Carallia*, and *Combretocarpus*; solitary and in small multiples and clusters; 1–2 per sq. mm. in the genera with large vessels, 6–20 per sq. mm. in *Crossostylis* and *Gynotroches*. Perforation plates simple; Marco (1439) notes some scalariform plates in the first-formed secondary xylem of *Gynotroches*. Intervascular

pitting scalariform in *Gynotroches*, alternate and moderately small in the other genera; pits to ray and wood parenchyma commonly elongated in various directions and also round and unilaterally compound; pits in *Anisophyllea* small and round only. Tyloses common, e.g. in *Anisophyllea* and *Carallia*;

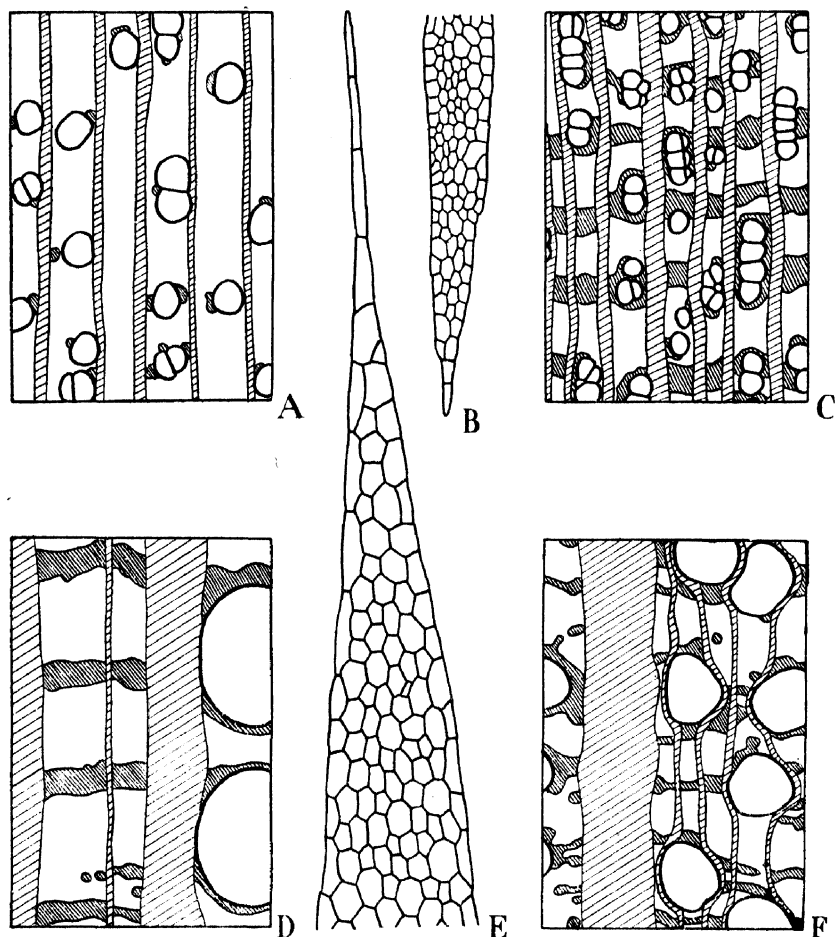


FIG. 134. RHIZOPHORACEAE

A, *Rhizophora conjugata* Linn. B, *Bruguiera parviflora* Wight et Arn. C, *Kandelia rheedii* Wight et Arn. D, *Anisophyllea laurina* R. Br. E, *A. laurina* R. Br. F, *Gynotroches axillaris* Blume.

sometimes with gummy deposits, e.g. *Carallia*, and, according to Marco (1439), often with chalky infiltrations completely occluding the lumina. Mean member length 0.7–1.0 mm. **Parenchyma** typically abundant and predominantly banded; the bands varying from moderately regular apotracheal forms in *Anisophyllea* (Fig. 134 D) and *Combretocarpus* p.p. to irregular and almost confluent (paratracheal) forms in some species of *Combretocarpus* and in *Carallia*, in which the bands tend to form arcs between the large rays but connect all the vessels and sometimes form wings from them; the bands vary

from several cells wide in *Carallia*, *Combretocarpus*, and *Anisophyllea* to 1 or 2 cells in *Gynotroches* (Fig. 134 F). Some paratracheal parenchyma always present and some isolated cells usually scattered among the fibres. Cells usually with dark gummy contents, crystals present in the ordinary cells in *Carallia* and in chambered cells on the edges of the bands and scattered among the fibres¹ in *Carallia* and *Combretocarpus*; silica present in *Combretocarpus motleyi* Hook. f. (794). Strands of 4–16, mostly 8 cells. **Rays** of 2 distinct sizes, the larger up to 10–15 cells wide; very high, commonly exceeding 5 mm.; often showing evidence of dissection into smaller units; uniseriate rays numerous and composed of upright cells; 4–10 rays per mm.; heterogeneous (Kribs's Types I and II A), with 2–10 marginal rows of high upright cells and some sheath cells. Cells commonly with dark gummy contents and with solitary crystals in *Carallia*. **Fibres** with small, flat, and sometimes rather indistinct borders, e.g. in *Anisophyllea*; walls very thick and often gelatinous. Mean length 1.8–2.6 mm.

GROUP III. *Anopyxis*, *Blepharistemma*, *Cassipourea*, *Macarisia*, *Sterigmapetalum* (Fig. 135 A, B, and E)

Vessels mostly small to medium-sized, 100–200 μ mean tangential diameter, approaching 200 μ mean tangential diameter in *Sterigmapetalum* and sometimes exceeding it in *Anopyxis*; exclusively solitary in *Anopyxis*, *Cassipourea*, and *Sterigmapetalum*; mostly 20–40 per sq. mm., sometimes more numerous in *Cassipourea*, rather fewer in *Sterigmapetalum*, and only about 4 per sq. mm. in some species of *Anopyxis*. Perforation plates typically both simple and scalariform, the latter with delicate bars, the simple perforations often much longer than wide and with parallel sides (1439). Intervascular pitting difficult to observe in genera with solitary vessels, according to Marco (1439) alternate to opposite and tending to scalariform in some genera; pits to ray cells and wood parenchyma typically large and elongated, varying from mostly both long and wide, e.g. in *Anopyxis*, to mostly round or slightly oval, as in some species of *Cassipourea*, sometimes unilaterally compound but mostly approximately the same shape and size as the subtending pits in the parenchyma walls; tending to be elongated horizontally in contact with wood parenchyma cells and irregularly in contact with ray cells. Sclerotic tyloses and amorphous deposits of gum present in some specimens of *Cassipourea elliptica* (1439) and thin-walled tyloses present in some other species of *Cassipourea*. Mean member length 1.0–1.4 mm. **Parenchyma** moderately abundant, typically predominantly paratracheal and absent from the adaxial sides of the vessels; varying from aliform, e.g. in *Anopyxis*, to aliform and confluent, with some diffuse, e.g. in some species of *Cassipourea*, or predominantly in uniseriate apotracheal bands, e.g. in *Blepharistemma*. With chambered crystal cells in some species of *Anopyxis*. Strands of 8–16 cells. **Rays** 2–5, mostly 3–4 cells wide, widest in *Anopyxis* and some species of *Cassipourea*; typically less than 1 mm. high, but rather higher in most species of *Cassipourea*; uniseriate rays numerous and composed of moderately to very high upright cells; mostly 5–12 rays per mm., sometimes slightly more numerous in *Blepharistemma* and *Cassipourea*; heterogeneous (Kribs's Types I and II A); with 4 or more marginal rows of upright cells, except in *Macarisia*, and with 10 or more rows

¹ Described by Marco (1439) as crystalliferous fibres.

in *Anopyxis* and *Cassipourea* p.p.; cells sometimes containing crystals. **Fibres** typically with large, distinctly bordered pits, tending to be more numerous on the radial walls; borders less distinct in *Blepharistemma* and *Macarisia*; walls thick and often gelatinous; mean length 1.6–2.2 mm.

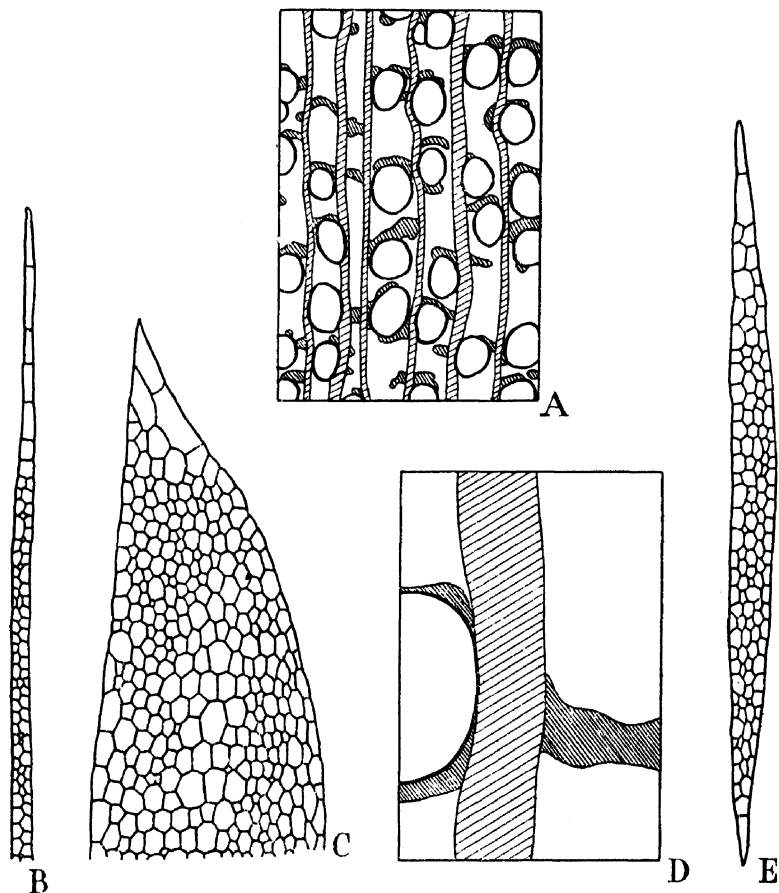


FIG. 135. RHIZOPHORACEAE

A, *Cassipourea podantha* Standley. B, C, *podantha* Standley. C, *Pellacalyx saccardianus* Scortech. D, *Poga oleosa* Pierre. E, *Anopyxis ealaensis* Sprague.

GROUP IV. *Pellacalyx* and *Poga* (Fig. 135 C and D)

These 2 genera do not fit satisfactorily into any of the other groups; their chief characteristics are given below.

Pellacalyx. **Vessels** medium-sized, arranged in tangential groups and rows, perforation plates simple and very occasionally delicately reticulate (1439), intervacular pitting large and opposite, pits to parenchyma similar or irregularly elongated, particularly to the ray cells; silica reported by Gonggrijp (794). **Parenchyma** enclosing the vessels and extending from them to form bands between the large rays, in narrower apotracheal bands and sometimes

scattered among the fibres. **Rays** up to 25 cells wide and very high; uniseriate numerous, composed of upright cells; heterogeneous. **Fibres** with bordered pits.

Poga. **Vessels** large (more than 200 μ) and almost exclusively solitary, fewer than 1 per sq. mm., perforations simple and nearly horizontal, intervascular pitting alternate, tending locally to conspicuous coalescent apertures, pits to parenchyma nearly always round but occasionally large, elongated and almost simple, sometimes unilaterally compound; mean member length about 8 mm. **Parenchyma** about the vessels, extending laterally from them in narrow wings and in apotracheal bands between the large rays. **Rays** of 2 distinct sizes, the larger up to 20 cells wide and very high, uniseriate rays numerous and low, heterogeneous. **Fibres** with a few distinctly bordered pits which are almost entirely limited to the radial walls, mean length about 2.0 mm.

ROOT

The well-known 'breathing' roots of members of the Rhizophoraceae inhabiting mangrove swamps have been the object of numerous investigations. The large intercellular spaces of the spongy **cortex** of these roots have for long been thought to facilitate gaseous exchange in the special habitat in which the plants grow. Troll (2282) has questioned this view, for he believes that the form of the root system in *Sonneratia* (Family Lythraceae) and *Bruguiera* is chiefly important because it enables a sequence of absorptive roots to be produced in a substratum of which the level is liable to be raised by the deposition of silt. Even Troll, however, subscribes to the previously accepted view to the extent of pointing out that the spongy structure of the cortical tissues may be of secondary importance in facilitating gaseous exchange. The root structure for each genus is described separately below.

(i) BRUGUIERA

Cortex thick, containing abundant, large, intercellular spaces, arranged radiately around the stele. According to Solereder, mechanical support is provided for this otherwise thin-walled tissue by annular, lignified thickening ridges to the cells which border on the intercellular spaces. In the light of Bowman's (252) observations on the similar structures which occur in *Rhizophora* (see next paragraph) it seems possible that they may represent cells filled with mucilaginous sap. Intercellular spaces are larger in the subterranean than in the aerial parts of the roots. Sclerenchymatous **idioblasts** occur in the cortical parenchyma. **Cork** consisting wholly of suberized cells below the ground, but of alternating layers of suberized and ordinary parenchymatous cells in the aerial portion.

(ii) RHIZOPHORA

Similar to *Bruguiera* but the primary **cortex** in the terrestrial part of the root is composed of cells of 2 kinds: (a) radially elongated cells connected with one another tangentially by short lateral arms; (b) rows of vertically elongated cells which exhibit small, circular lumina in transverse sections. Solereder, in common with other early authors, records the existence of ridges of thickening which are said to give mechanical support to the radially elongated cells in which they are alleged to occur, but according to the more

recent work of Bowman (252) these 'Verdickungsleisten' are really cells filled with mucilaginous sap. Mullan (1570) states that the cortex in the aerial part of the root system of *R. mucronata* Lam. is much reduced and the lacunae small, whilst the component cells are all alike and roundish to polygonal in outline. Bowman (l.c.) also says that the cortex in the subterranean clusters of roots, which lie below the mud but are attached to the ends of the stilt roots, is composed of round cells interspersed with large intercellular spaces. Some of these cells are arranged in short strands, but others radiate from a central cell, the latter often being filled with starch and those of the radii with mucilage. H-shaped, sclerenchymatous idioblasts project into the cortical intercellular spaces in the aerial part of the root, but are less numerous below ground. Mullan (l.c.) records the existence of vertically elongated tubular cells, filled with tannin and oil, situated at the junctions between the branched cells in the terrestrial part of the root of *R. mucronata*.

(iii) CERIOPS

Mullan (1570) describes the general structure of the root system of *Ceriops candolleana* Arn. as similar to that of *Rhizophora mucronata*, except that, in *Ceriops*, multiradiate idioblasts are absent from the cortex.

(iv) CARALLIA

Buscalioni (317) has described the morphology and anatomy of a fasciated aerial root of *Carallia integerrima* DC.

For further details concerning the root system of mangroves belonging to the Rhizophoraceae see Liebau (1368) and Emould (627).

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Examination of the exomorphic and anatomical features of *Anopyxis ealaensis* Sprague by Sprague and Boodle (2173) led to the conclusions that this species has many features in common with the Rhizophoraceae-Legnotideae, the agreement with *Macarisia pyramidata* Thouars being particularly close.

(ii) FROM WOOD STRUCTURE

According to Marco (1439), the wood structure does not fully conform with any of the 3 taxonomic systems proposed by Bentham and Hooker, Ridley, and Schimper. The tidal genera, *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*, form a well-defined, homogeneous natural group, which is readily separable from other members of this or any other family. The Legnotideae (the inland genera), as proposed by Bentham and Hooker, includes woods of very different types, which Marco has separated into 2 groups, which he terms the Macarisieae and the Gynotrocheae. These groups, which correspond to Groups II and III in the above description of the wood, he considers as being as well-defined and natural aggregations as the Rhizophoreae. The material examined by the author fully supports his treatment of the Rhizophoreae, but provides less convincing evidence of the clear distinction between the Gynotrocheae and Macarisieae.

Marco expresses some doubts as to the placing of *Anopyxis* and *Sterigma-*

petalum in the family and only places them provisionally in the Macarisieae. They appear to fit reasonably well in this group. He excludes *Poga* and *Pellacalyx* and notes a superficial resemblance between the latter and *Embothrium* of the Proteaceae. Both these genera, however, have many characteristics in common with other genera in this family; indeed, nearly all the details of their structure can be matched in some species in the family, though it is true that neither genus fits very well into any of the proposed groups.

Panshin (1649), in a study of the woods of the Philippine mangrove swamps, found no evidence of the anatomical structure of the wood being influenced by the habitat.

ECONOMIC USES

Apart from the timbers derived from the family, the tanniniferous bark of *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* is one of the most important economic products. This material is imported into European countries for commercial use, although the tanning qualities are said to be inferior to those of many other materials. The microscopy and chemical composition of mangrove barks have been exhaustively described by Wenzel (2412), who gives an extensive bibliography of other work on the same subject. According to Bodensstab (211) commercial samples of *Rhizophora* bark consist of hard, heavy pieces, 3–30 mm. thick, with little or no cork. The colour is red to dark brown throughout, and the taste and scent weakly aromatic. Fracture brittle and horny. Cork, mostly confined to young material, up to 2 mm. thick, composed of thin-walled cells with brownish contents. A layer of parenchyma 1–5 mm. thick beneath the cork includes fairly numerous stone cells, the latter being solitary and in groups and provided with branched pits in the concentrically zoned thickening of the cell walls. Groups of stone cells towards the inside of the bark more elongated than those towards the exterior, appearing to the naked eye as lines or bars. Cells containing solitary crystals occur at the periphery of the groups of stone cells. Ground tissue consisting of medullary rays, 5–6 cells wide, which contain abundant cluster crystals, and of phloem strands which include occasional short thick fibres. All parenchymatous tissues contain tannin and a brownish-red colouring matter.

The family is not important as a source of timber, but the 'tidal' genera are often in demand as poles and for making charcoal. *Carallia lucida* Roxb. is used as a general construction timber in India and to some extent for ornamental purposes, making use of its oak-like silver grain.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Anisophyllea, Anopyxis, Blepharistemma, *Bruguiera*,* *Carallia*, *Cassipourea*, *Ceriops*, *Crossostylis*, *Dactylopetalum*, *Gynotroches*, *Kandelia*, *Macarisia*, *Poga*, *Rhizophora*, *Weihea*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Anisophyllea, Anopyxis, Blepharistemma, *Bruguiera*, *Carallia*, *Cassipourea*,

Ceriops, Combretocarpus, Crossostylis, Gynotroches, Kandelia, Macarisia, Pellacalyx, Poga, Rhizophora, Sterigmapetalum.

LITERATURE

(i) *On General Anatomy*

Arzt 45, Bodenstab 211, Bowman 251, 252, Buscalioni 317, Emould 627, Engler 633, Liebau 1368, Mullan 1570, Sprague and Boodle 2173, Troll 2282, Wenzel 2412.

(ii) *On Wood Structure*

Becking *et al.* 164, Benoist 170, den Berger 179, 182, Besson 186, Burgerstein 310, Cooper and Record 461, Dadswell and Record 533, Foxworthy 705, Gonggrijp 794, Hopkinson 1083, Howard 1088, Janssonius 1154, Jentsch 1173, Kanehira 1204, 1206, Kribs 1283, Lecomte 1334, Marco 1439, Mériaud 1492, Panshin 1649, Pearson and Brown 1679, Pfeiffer, J. Ph. 1713, Record 1783, 1851, Record and Hess 1886, Record and Mell 1894, Riera 1937, Stone 2202, Tupper 2295.

135. COMBRETACEAE

(FIG. 131 on p. 598; FIG. 136 on p. 614; FIG. 137 on p. 616)

SUMMARY

(i) GENERAL

A mainly tropical family of trees, shrubs, and woody climbers. The **leaf** is dorsiventral, or more rarely centric, and provided with glandular and non-glandular **hairs** of various kinds. Of these the simple unicellular and unicellular 2-armed types are the most widespread. The leaf **stomata** are usually confined to the lower surface, but occur on the upper side also in a few species; they are ranunculaceous. The **mesophyll**, in some genera, includes ramifying sclerenchymatous fibres which are generally connected with the vascular bundles of the veins. Large stellate idioblasts containing cluster crystals have also been recorded in the mesophyll. These idioblasts are sometimes apparent as transparent dots if the leaf is not too thick. Cluster **crystals** also occur in the parenchymatous tissues in other parts of the plant. The vascular bundles of the **veins** are nearly always bicollateral, and accompanied by a varying amount of sclerenchyma in different genera and species. Canal-like **secretory receptacles** are present in association with the xylem of the veins in a number of species of *Terminalia*. **Cork** in the young stem arises superficially or in the pericycle in different genera and species. The secondary **phloem** is frequently characterized by islands of sclerenchyma, the latter including chambered fibres filled with crystals. Both **interxylary** and **intra-xylary phloem** are common in the family. Negatively geotropic **roots**, with abundant intercellular spaces in the cortex, have been recorded in *Laguncularia* and *Lumnitzera*.

(ii) Wood

Vessels mostly medium-sized, either exclusively solitary or with numerous multiples of 4 or more cells, perforations simple, intervacular pitting alternate, pits to parenchyma similar to the intervacular pitting; vested; members of medium length. **Parenchyma** typically aliform to confluent with some scattered cells, occasionally vasicentric and in terminal bands; idioblasts containing druses present in some genera. **Rays** most typically exclusively

uniseriate or rarely biseriate, but up to 2-5 cells wide in several species, particularly of *Terminalia*; homogeneous or slightly heterogeneous; crystals, either single or druses, commonly present. **Fibres** with small simple pits, some fibres usually septate, of medium length. **Vasicentric tracheids** present in 1 genus. Traumatic vertical **intercellular canals** occasionally present. **Included phloem** of the 'foraminate' type present in 4 genera.

LEAF

Usually dorsiventral; rarely centric; middle of the mesophyll composed of aqueous tissue surrounded by palisade in species of *Laguncularia* and *Lumnitzera*.

Hairs

- (a) Non-glandular. (i) Simple, unicellular, often somewhat bulbous at the base and with a cellulose membrane more or less conically or convexly arched outwards towards the filamentous distal end; sometimes appearing to be bicellular owing to this peculiar construction (Fig. 136 A-B). This type is widely distributed. (ii) Unicellular, 2-armed in *Conocarpus* (Fig. 136 C); sometimes with an imperfectly developed second arm in *Ramatuela* and *Terminalia* (Fig. 136 D).

(b) Glandular

I. Sessile or short-stalked. (i) Spherical, bladder-like, the material secreted between the cuticle and the surface of the component cells obscuring the internal structure of the gland in *Calycopteris* (Fig. 136 E), *Combretum* (pro parte), *Guiera*. (ii) Small glandular scales, with little or no accumulation of secreted material in *Combretum* (pro parte) (Fig. 136 F) and *Thiloa*.

II. With a more or less elongated stalk. (i) With a spherical or ellipsoidal head in *Cacoucia*, *Combretum* (species at one time included in the genus *Poivreia*), *Quisqualis*.

- (c) Almost sessile, cap-shaped glands, situated at the bases of flask-shaped cavities, recorded on both leaf surfaces in *Languncularia racemosa* Gaertn. (Fig. 136 H-I); and somewhat similar ones on the lower side of the leaf of *Conocarpus erectus* Linn. Large, conspicuous glands also occur on the petiole in *Anogeissus*, *Conocarpus*, *Laguncularia*, *Terminalia*. Reddish glandular scales situated in small pits recorded by Hate (1919) on the lower surface of the leaf in *Calycopteris floribunda* Lamb. The anatomy and development of the petiolar **thorns** of *Quisqualis indica* Linn. have been described by Helm (1946).

Epidermis papillose on the lower surface of 2 species of *Combretum*; with marginal pits to the cell walls in a number of species of *Combretum* and in *Ramatuela*. **Hypoderm** said to occur locally below the upper epidermis in *Combretum ternatum* Wall. **Stomata** ranunculaceous; usually confined to the lower surface, but present on the upper side as well in a few species of *Combretum*, *Conocarpus*, *Guiera*, *Laguncularia*, *Lumnitzera*, *Macropteranthes*. **Hydathodes** recorded in *Laguncularia* and *Lumnitzera*. Sclerenchymatous fibres, branching off from the veins and extending irregularly throughout the

mesophyll, present in species of *Anogeissus*, *Buchenavia*, *Bucida*, *Combretum*, *Ramatuella*, *Thiloa*. Vascular bundles of the larger **veins** bicollateral; enclosed by a ring or accompanied by an arc of sclerenchyma in species of *Anogeissus*, *Cacoucia*, *Combretum*, *Conocarpus*, *Guiera*, *Macropteranthes*, *Quisqualis*, *Ramatuella*, *Terminalia*, *Thiloa*; accompanied by only a few fibres in species of *Calycopteris*, *Combretum*, *Macropteranthes*, *Terminalia*; scleren-

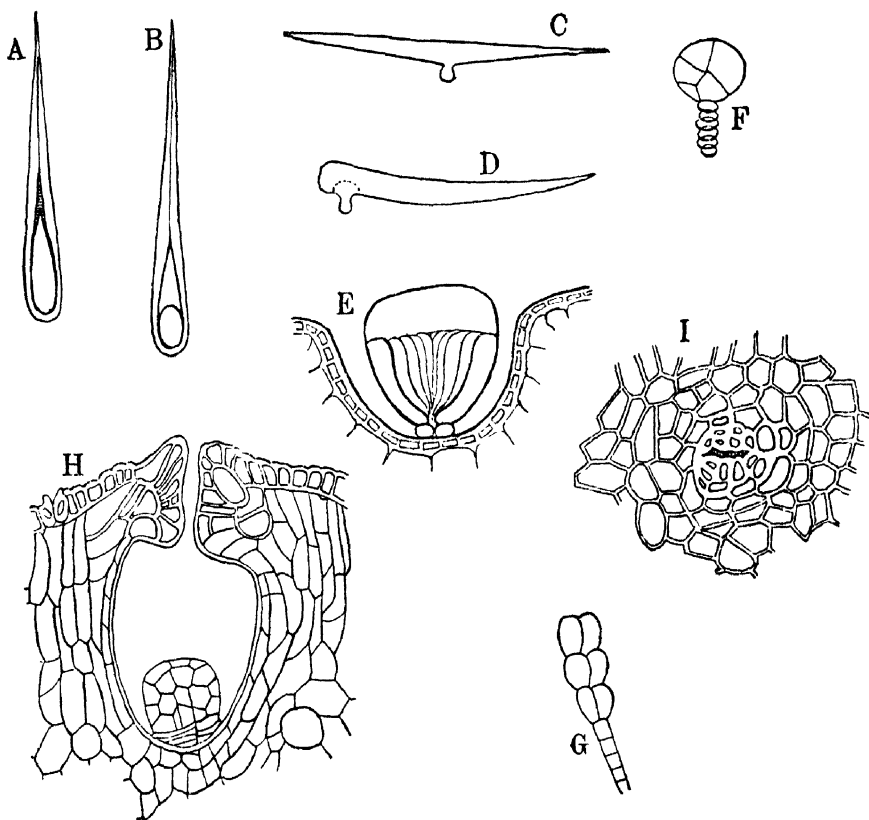


FIG. 136. COMBRETACEAE

A, B, Ordinary combretaceous hairs. C, Two-armed hair of *Conocarpus*. D, One-armed hair of *Terminalia argentea* Mart. E, Glandular hair of *Calycopteris* in section. F, External gland of *Combretum aculeatum* Vent. G, External gland of *Combretum decandrum*, Roxb. H, I, Glandular leaf-pit of *Laguncularia racemosa* Gaertn. f.—A, G, after Heiden; H, I, after Holtermann.

chyma absent from the veins in certain species of *Combretum*, *Lumnitzera*, *Terminalia*. Vascular bundles of the smaller veins embedded in the mesophyll in species of *Anogeissus*, *Combretum*, *Conocarpus*, *Laguncularia*, *Lumnitzera*, *Ramatuella*, *Terminalia*, *Thiloa*, or vertically transcurrent by sclerenchyma or thin-walled tissue in different species; accompanied by a large or small amount of sclerenchyma in species of *Anogeissus*, *Cacoucia*, *Combretum*, *Guiera*, *Macropteranthes*, *Quisqualis*, *Ramatuella*, *Terminalia*, *Thiloa*; sclerenchyma absent from species of *Anogeissus*, *Calycopteris*, *Combretum*, *Laguncularia*, *Lumnitzera*, *Macropteranthes*, *Terminalia*.

Petiole. Transverse sections through the distal end, in the few species of *Calycopteris* (Fig. 131 C) and *Combretum* represented in the Kew slide collection, exhibiting a solitary crescent-shaped vascular strand, with outwardly directed or incurved ends. Main vascular strand closed and dorsally flattened in *Terminalia chebula* Retz. (Fig. 131 A). Canal-like **secretory cavities**, provided with a definite epithelium and filled with mucilaginous contents, situated above the xylem of the veins and extending into the mesophyll of a number of species of *Terminalia*. Similar cavities also seen in the 'cortical' region of the petiole of *Terminalia chebula*. **Secretory cells**, with unidentified amorphous contents, observed in unlignified tissue in species of *Calycopteris*, *Combretum*, and *Terminalia*, and probably present in other genera and species as well. **Fatty bodies** often present in the mesophyll. **Crystals** almost exclusively clustered; occurring in the mesophyll and beside the vascular bundles of the veins; numerous, large, solitary types noted in the 'cortical' region of the petiole in *Terminalia chebula*; sometimes situated in large, somewhat star-shaped idioblasts, the latter being visible as transparent dots if the leaf is not too thick, in species of *Anogeissus*, *Combretum*, *Conocarpus*, *Guiera*, *Laguncularia*, *Macropteranthes*, *Quisqualis*, *Terminalia*, *Thiloa*.

AXIS

YOUNG STEM (Fig. 131 B and D)

Cork arising superficially in certain species of *Anogeissus*, *Calycopteris*, *Conocarpus*, *Laguncularia*, *Lumnitzera*, *Macropteranthes*, and *Terminalia*; originating in the pericycle in other species of *Anogeissus*, *Calycopteris*, *Conocarpus*, and *Terminalia* as well as in *Cacoucia*, *Combretum*, *Guiera*, *Quisqualis*, *Ramatuela*, *Thiloa*; consisting mostly of cells with wide lumina and thin walls, but sometimes including stone cells or cells thickened only on one side. Cork cells radially elongated in *Quisqualis*. Phelloid cells stated to be included in the cork of the same genus. **Pericycle** usually containing isolated strands of fibres situated around a broad inner parenchymatous portion. Secondary **phloem** frequently characterized by islands of sclerenchymatous elements; including chambered fibres filled with small clustered crystals and arranged in tangential bands as seen in transverse sections of species of *Anogeissus*, *Combretum*, *Conocarpus*, *Laguncularia*, *Lumnitzera*, *Quisqualis*, *Terminalia*, *Thiloa*. Phloem and **xylem** in most genera forming a continuous cylinder traversed by narrow rays. Vessels with simple perforations. Strands of **interxylary phloem**, sometimes arranged in concentric circles and composed of soft tissue, often containing numerous clustered crystals, recorded in species of *Calycopteris*, *Combretum* (particularly in African species), *Guiera*, *Thiloa*. For further details see under 'Wood' on p. 618. **Intraxylary phloem**, either in the form of a ring or in separate strands at the periphery of the pith, recorded in species of *Anogeissus*, *Cacoucia*, *Calycopteris*, *Combretum*, *Guiera*, *Laguncularia* (inconspicuous), *Lumnitzera* (inconspicuous), *Pteleopsis*, *Quisqualis*, *Ramatuela*, *Terminalia*, *Thiloa*. Mucilage cavities recorded in the intraxylary phloem of various species of *Terminalia*, and in the interxylary phloem in species of *Combretum*. **Pith** usually fairly small, mostly consisting of lignified, fairly thick-walled, or, more rarely, of thin-walled cells; containing groups of stone cells in *Calycopteris* and *Terminalia* sp. and vertically elongated elements filled with an

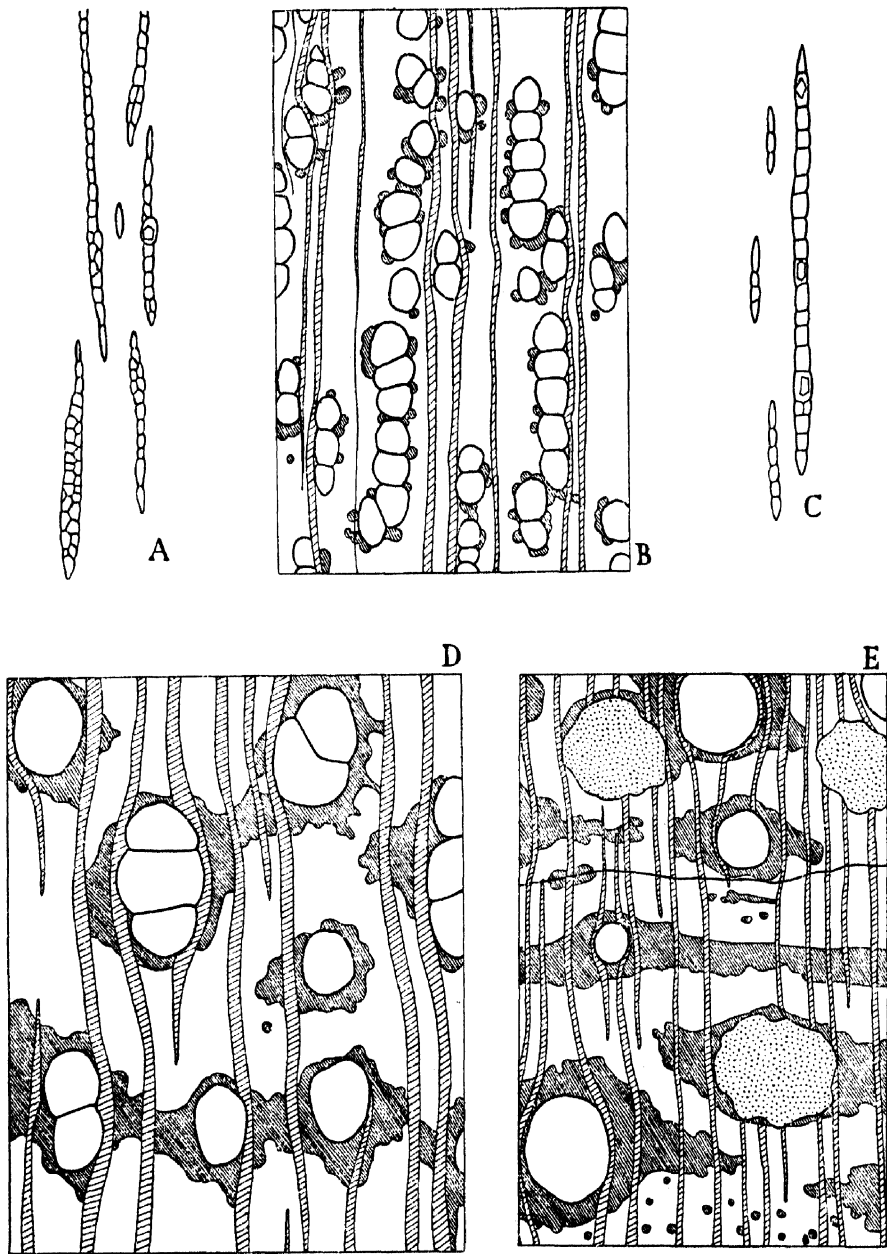


FIG. 137. COMBRETACEAE

A, *Guiera senegalensis* Lam. B, *Lumnitzera coccinea* Wight et Arn. C, *Terminalia parviflora* Presl.
D, *T. ivorensis* A. Chev. E, *Combretum hartmannianum* Schweinf.

unidentified white substance in several species of *Combretum*. **Secretory elements.** Mucilage canals recorded in the pith in a number of species of *Terminalia*; cavities observed in the cortex and phloem in species of *Calycopteris* and *Terminalia* (see also under 'Intraxylary Phloem'). Secretory cells with unidentified, amorphous contents seen in certain species of *Combretum*. **Crystals** mostly clustered; solitary types less frequent; very small raphides noted in the phloem of *Calycopteris* (see also under 'Phloem' and 'Interxylary Phloem' above).

WOOD (Fig. 137)

Vessels mostly medium-sized (mean tang. diam. 100–200 μ), moderately small (50–100 μ) in *Anogeissus leiocarpus* Guill. et Perr. and *Lumnitzera*, large (about 280 μ) in *Strephonema*; exclusively solitary in *Combretum*, *Guiera*, *Ramatuela* (931 A) and *Strephonema*, with radial multiples of 4 to several cells in *Anogeissus* and *Lumnitzera* (Fig. 137 B); the beginning of the ring marked by a zone without vessels in some species of *Terminalia*; mostly 5–20 per sq. mm., fewer than 5 per sq. mm. in *Combretum* p.p., *Strephonema* and most species of *Terminalia*, about 20 per sq. mm. or slightly more in some species of *Anogeissus*, *Conocarpus*, and *Lumnitzera*; according to Record (1851) ring-porous in some species of *Combretum*. Perforations simple. Intervascular pitting alternate, medium-sized or occasionally rather small, e.g. in *Lumnitzera* and *Pteleopsis*, sometimes with striations due to coalescent apertures, e.g. in *Buchanavia*; pits to parenchyma similar to the intervacular pitting, pits to ray cells sometimes arranged in distinct horizontal rows, e.g. in *Combretum*. Pits vested (78). Tyloses abundant in *Terminalia*, deposits of gum common and sometimes abundant, white chalky deposits noted by Panshin (1649) in *Lumnitzera*. Mean member length 0.3–0.5 mm. **Parenchyma** predominantly paratracheal, typically abundant, aliform to confluent and with some isolated cells scattered among the fibres (Fig. 137 D and E); the paratracheal parenchyma varying from a few cells round the vessels, e.g. in most species of *Lumnitzera* (Fig. 137 B), to broad, irregular confluent bands, these bands more regular and possibly apotracheal in some species of *Terminalia*, e.g. *T. bialata* Steudel; with both aliform parenchyma and isolated patches suggesting vestiges of continuous broad bands in *Strephonema*; narrow terminal¹ bands sometimes present in *Buchanavia*, *Bucida*, and *Terminalia*. Without crystals in most genera but chambered crystalliferous cells common in *Pteleopsis*, large single crystals present in chambered or ordinary cells in some species of *Terminalia*, and with large idioblasts containing druses in some species of *Combretum*, *Guiera*, and *Terminalia* (e.g. *T. catappa* L.); small druses also present in the parenchyma surrounding the strands of included phloem in *Guiera*; commonly with gummy contents. Strands commonly of 6–8 cells. Solereder refers to the presence of unligified parenchyma in the twining plant *Quisqualis indica* Linn. **Rays** exclusively uniseriate or with occasional biseriate portions in *Anogeissus* (most species), *Buchanavia*, *Combretum* p.p., *Conocarpus*, *Laguncularia*, *Lumnitzera*, and *Terminalia* p.p. (e.g. *T. arjuna* Bedd., *T. belerica* Roxb., *T. bialata* Steudel, *T. curtisii*

¹ Chowdhury (412–14) has shown that in *Terminalia tomentosa* W. et A. these bands are the first tissue formed in the growth ring and has suggested the term 'initial' in place of 'terminal'.

Ridl., *T. excelsa* Liebm., *T. mannii* King (1679), *T. myriocarpa* Heurck et Muell. (1679), *T. obovata* (R. et P.) Steud., *T. oliveri* Rands (1679), *T. paniculata* Roth., *T. pyrifolia* Kurz., *T. subspathulata* King, *T. superba* Engl. et Diels, *T. teysmannii* Koord. et Val. (1154), and *T. tomentosa* Wight et Arn.), commonly 2 cells wide in *Combretum* (a few species), *Guiera*, *Pteleopsis*, and *Strephonema*, 2-4 cells wide in *Bucida* and many species of *Terminalia*, up to 5 cells wide in *Quisqualis* (2158); less than 1 mm. high; uniseriate moderately numerous in woods with multiseriate rays and composed of procumbent cells; mostly 8-12 rays per mm., more numerous (12-18) in *Anogeissus* and some species of *Combretum*, *Guiera*, *Laguncularia*, and *Lumnitzera* (1649), about 4-6 per mm. in a few species of *Terminalia*, e.g. *T. ivorensis* A. Chev.; homogeneous (Kribs's Types I and III) in *Buchenavia*, *Bucida* (apart from crystalliferous cells), *Combretum* (a few species), *Pteleopsis*, and most species of *Terminalia*; heterogeneous in the remainder but not markedly so, except in *Strephonema*, with 4 or more marginal rows of square or upright cells and uniseriate rays composed entirely of upright cells, and, according to Record and Hess (1886), in *Ramatuella*; rays composed entirely of square or upright cells in *Terminalia* p.p. Crystals common in *Anogeissus*, *Bucida*, *Combretum* p.p., and *Terminalia* p.p. (particularly in species with uniseriate rays), mostly as single crystals in square cells interspersed in rows between the procumbent cells (Fig. 137 c), the crystalliferous cells often conspicuous in tangential sections (particularly in *Bucida*) owing to their larger size or rounded shape (Fig. 137 A); large idioblasts containing druses present in *Guiera*; gummy deposits often present, conspicuous in *Lumnitzera*. **Fibres** typically with small, often very inconspicuous, simple pits, more numerous on the radial than on the tangential walls; pits with small borders in *Lumnitzera* and, according to Holterman as quoted by Solereder, in *Combretum decandrum* Roxb. A proportion of the fibres septate in some species of *Anogeissus*, *Combretum*, *Conocarpus*, *Guiera* (2158), *Pteleopsis*, *Strephonema*, and *Terminalia*, the septate fibres sometimes more numerous in the neighbourhood of the parenchyma and, according to Solereder, sometimes containing crystals in *Combretum* and *Terminalia*. Walls moderately to very thick. Mean length 0.8-1.7 mm. **Vasicentric tracheids** present in *Strephonema*. **Intercellular canals** of the vertical traumatic type present in some specimens of *Anogeissus*, *Buchenavia*, *Bucida*, and *Terminalia*. **Growth rings**. The seasonal development of the wood of *Terminalia* has been investigated by Coster (481) and Chowdhury (412-14). Chowdhury has shown that in *T. tomentosa* the so-called 'terminal' band of parenchyma is in fact the first-formed tissue of the growing season. Heiden (2158) refers to **secretory spaces**, with yellow contents that give a mucilage reaction, in thick parts of branches of *Terminalia bellerica* Roxb. and *T. macroptera* Mart. **Included (interxylary) phloem** of the 'foraminate' type (c. l. *foraminulatum*) present in some species of *Calycopteris* (2158), *Combretum*¹ (Fig. 137 E), *Guiera*, and *Thiloa* (2158); the strands of included phloem usually isolated, though tending to occur in tangential rings, particularly in *Thiloa* (1679), and occasionally linked by

¹ Solereder (2158) notes that included phloem occurs only in the African species of *Combretum* and lists the following: *C. erythrophyllum* Sond., *C. hartmannianum* Schweinf., *C. kraussii* Hochst., *C. lepidotum* Rich., *C. nyikae* Engl., *C. rueppellianum* Rich., *C. salicifolium* E. Mey., *C. schelei* Engl., *C. tenuispicatum* Engl., *C. tricanthum* Fres. To these may be added *C. multispicatum* Engl. et Diels and *C. guemzii* Sond.

parenchyma; radial strands occur occasionally in the rays in *Combretum*. The strands contain no bast fibres; the parenchyma often contains numerous small druses, e.g. in *Guiera*. For inter- and intraxylary phloem see also under 'Young Stem'.

ROOT

Negatively geotropic roots, with abundant intercellular spaces in the **cortex**, recorded in *Laguncularia racemosa* Gaertn. and *Lumnitzera racemosa* Willd.

TAXONOMIC NOTES

The wood structure is very uniform throughout the family. *Guiera* and *Lumnitzera* are slightly exceptional in having only scanty paratracheal parenchyma and the latter is further distinguished by its radial vessel multiples. It is of interest that the occurrence of included phloem in *Combretum* appears to be limited to African species, not all of which, however, possess this character.

ECONOMIC USES

Myrobalans are the fruits of *Terminalia chebula* Retz. and Indian Almonds the seeds of *T. catappa* Linn. Infusions of the leaves and young stem of *Combretum micranthum* G. Don. are used by the natives in western tropical Africa for fevers and internal complaints generally. Leaves and young twigs, believed to have been derived from this species and submitted to Kew for identification, showed the following features. Leaves mucronate, opposite, somewhat glaucous on the upper surface, but bearing peltate, often yellow, scales on the lower side. Mesophyll dorsiventral, containing particularly large cluster crystals in special cavities. Petiole, in transverse sections through the distal end, exhibiting a solitary, arc-shaped vascular strand with incurved ends, the xylem vessels being numerous and arranged in radial rows. In the young stem of the same species intraxylary phloem occurs on the inside of the closed cylinder of xylem. Vessels small, solitary, or tending to be in radial rows. The pericycle contains few fibres, and the broad phloem includes numerous cluster crystals. Cork deep-seated in origin. Pith containing a few stone cells.

The timbers of some species of *Terminalia* are well known to commerce, though perhaps not used in any very large quantities, e.g. Indian Laurel, *T. alata* Roth., Indian Silver Grey Wood, *T. bialata* Steud., and 2 West African species, Idigbo, *T. ivorensis* A. Chev., and Afara or Limba, *T. superba* Engl. et Diels. These and other species of *Terminalia* and of *Anogeissus*, however, may be of considerable importance locally. Gamble (737) said of *T. tomentosa* Wight et Arn., 'it is possible that there is no tree in the Indian forests . . . so important for the supply of the agricultural population'.

The wood of *Anogeissus* spp. is used in India for the axles, shafts, and wheel-spokes of carts, and that of *Bucida buceras* Linn. is valued in the West Indies as a durable construction timber.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Anogeissus, Buchenavia, Bucida, Cacoucia, Calycopteris,* Combretum,* Conocarpus, Guiera, Laguncularia, Lumnitzeria, Macropteranthes, Pteleopsis, Quisqualis, Ramatuela, Terminalia,* Thiloo.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Anogeissus, Buchenavia, Bucida, (Calycopteris), Combretum, Conocarpus, Guiera, Laguncularia, Lumnitzeria, Pteleopsis, (Quisqualis), (Ramatuela), Strephonema, Terminalia, (Thiloo).

LITERATURE

(i) *On General Anatomy*

Hate 919, Helm 946.

(ii) *On Wood Structure*

Bailey 73, 78, Bastos 147, Becking *et al.* 164, Benoist 170, den Berger 179, 182, Besson 186, British Honduras For. Department 274, Brown, F. B. H. 282, Burgerstein 310, 312, Chalk *et al.* 364, Chalk and Chattaway 362, Chowdhury 412-14, Cooper and Record 461, Coster 481, 482, Desch, H. E. 574, Foxworthy 705, Gamble 737, Hopkinson 1083, Howard 1088, Janssonius 1154, Jentsch 1171, Jones 1191, Kanehira 1206, 1209, Lecomte 1334, Méniaud 1492, Panshin 1649, Pearson and Brown 1679, Pfeiffer, H. 1712, Record 1780, 1783, 1787, 1801, 1818, 1825, 1834, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Riera 1937, Stone 2206, 2207, Torres 2269, Williams 2430.

136. MYRTACEAE

(FIG. 138 on p. 622; FIG. 139 on p. 624; FIG. 140 on p. 626; FIG. 141 on p. 628)

SUMMARY

(i) GENERAL

Trees or shrubs from tropical and sub-tropical regions; particularly common in Australia. A noteworthy feature is the presence of **secretory cavities**, which are lined with epithelium when young, and almost invariably secrete oily substances. According to Welch (2395) the epithelial layer is not conspicuous in the species of *Eucalyptus* which he examined. The same author also concluded that the cavities are mainly schizolysigenous in origin. The cavities are to be found below the epidermis on either side of the leaf, and when in this position appear as transparent dots. In some instances they are enclosed in emergences. They also occur in the ground tissue of the young stem, particularly the cortex, but have not been recorded in the root. The **mesophyll** is often isobilateral to centric, especially in those species where the lamina of some or all of the leaves normally assumes a vertical position. The **hairs** are mostly unicellular, or sometimes apparently with 2 chambers, thus resembling those of the Combretaceae; in a few genera they tend to be or are 2-armed. The **stomata** are usually ranunculaceous except in a few species, and occur on both surfaces of vertically placed leaves. The **cork** is often stratified, and partly composed of phelloid cells. The secondary **phloem** consists of alternating layers of fibrous and non-fibrous tissue except in a few genera. The **vascular bundles** of the young stem, as well as those

of the petiole, are bicollateral in all investigated species. **Intraxylary** phloem is believed to be universally present. **Tannin** is abundant in the tissues. Both solitary and clustered **crystals** occur.

(ii) Wood

Vessels most typically small, numerous, solitary and without definite arrangement, but medium-sized to large, fewer, with numerous multiples and a marked tendency to an oblique or radial pattern in some genera, particularly *Eucalyptus*; perforations simple, intervacular pitting alternate except in 2 genera, vested, commonly minute and with pits to ray cells similar, but sometimes larger and with oblong pits to ray cells; members of medium length. **Parenchyma** typically diffuse or in uniseriate bands in the woods with solitary vessels, predominantly paratracheal in woods with numerous multiples, with some intermediate forms with both diffuse and paratracheal types or with broader bands apparently intermediate between metatracheal and confluent. **Rays** exclusively uniseriate or up to 2-6 (mostly 2-3) cells wide; usually moderately heterogeneous, occasionally markedly so, sometimes homogeneous. **Fibres** typically with distinctly bordered pits; moderately short to moderately long, but usually of medium length. **Vasicentric tracheids** commonly present. **Intercellular canals** of the vertical traumatic type present in a few genera.

LEAF

Often isobilateral or centric, particularly in vertically placed leaves such as those of *Callistemon linearis* DC. and in cylindrical leaves like those of *Calothamnus* (Fig. 139 H), the centre of the leaf being occupied by aqueous tissue in the last genus. Species of *Eucalyptus* and *Eugenia* possessing both vertical and horizontal leaves sometimes exhibit isobilateral structure in the former but are dorsiventral in the latter. According to Ohtani (1936) mechanical tissue occurs in the leaf margin in *Eucalyptus* and *Melaleuca* and to a lesser extent in *Eugenia* and *Pimenta*. **Hairs** usually simple, unicellular or apparently 2-chambered, the structure in the last instance somewhat recalling that of hairs in the Combretaceae; sometimes 2-armed or with a tendency towards that structure in *Calyptanthus*, *Eugenia*, *Myrcia*. Glandular hairs absent. **Cork warts**, resembling lenticels, recorded in *Eucalyptus* and *Eugenia*; their mode of development in *Eucalyptus globulus* Lab. has been described by Motte (1966). **Epidermis** coated with wax in some species of *Eucalyptus*. **Stomata** usually occur on all parts of the surface of leaves with isobilateral or centric structure; ranunculaceous in most instances, but rubiaceous in *Myrcia*, and, according to Bandulska (1932), in *Rhodomyrtus*. The epidermal cells and stomata of *Rhodomyrtus* and *Tristania* have been described in considerable detail by Bandulska (l.c.). Stomata of *Darwinia grandiflora* Baker et Smith described by these authors (1912) as having guard cells shaped in transverse section like the arms of a pair of callipers. **Hypoderm** stated to occur below the upper epidermis in several species of *Metrosideros* and *Psidium*; crystalliferous in *P. guajava* Linn. according to de Boer (1914). **Mesophyll** said to contain sclerenchymatous fibres in *Jambosa* sp. and stone cells in certain species of *Eugenia*. Johnson (1918) has described differences in the mesophyll structure of horizontal and vertical leaves of

Eucalyptus globulus. Elongated water-storage tracheids with spiral thickening recorded by Baker and Smith (112) at the boundary between the palisade and loose spongy tissue in the centric leaf of *Darwinia grandiflora* Baker et Smith. **Petiole** (Fig. 139 A-D and F). Transverse sections through the distal end in the few species of *Callistemon*, *Eucalyptus*, *Eugenia*, *Feijoa*, *Myrtus*, *Pimenta*, and *Syncarpia* represented in the Kew slide collection exhibit a single, principal, arc-shaped vascular strand, which is widely open, U-shaped, or with somewhat incurved ends according to the species. Additional strands in the wings observed in *Eugenia caryophyllus* (Sprengel) Sprague (syn. *E. caryophyllata* Thunb.). Main vascular strand apparently bicollateral in all species

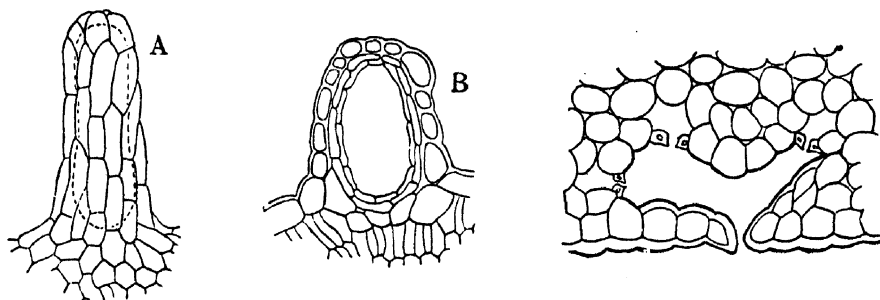


FIG. 138. MYRTACEAE, A-B; MELASTOMACEAE, C

A, B, Secretory cavity in an emergence of the leaf of *Eucalyptus maculata* var. *citriodora* Hook. C, Stomatal pit of *Mouriria eugeniaefolia* Spruce.—A-B, after Lignier; C, after van Tieghem.

examined, but adaxial phloem not always very clearly defined; generally surrounded by a continuous sheath of fibres varying in width in different species. Solitary and clustered **crystals** common in all unligified tissues. Crystal-sand also recorded by de Boer (214) in the cortical region of the petiole of *Psidium guajava*. **Secretory elements**. Cells containing tannin abundant in all unligified tissues. The family is characterized by secretory cavities (see also 'Axis') with various kinds of, but generally oily, contents (said to be filled with mucilage in *Tristania laurina* R. Br.); situated below the epidermis, usually on both sides of the leaf; also observed in the cortical region of the petiole in the few species represented in the Kew slide collection; enclosed in emergences in a few species, e.g. in young leaves of *Eucalyptus maculata* var. *citriodora* Hook. (Fig. 138 A-B). Similar nodules, but surmounted by tufts of long hairs, recorded by Fourment and Melis (702) in *E. erythrocorys* F. v. M. and *E. preissiana* Schau. and by shorter hairs in '*E. spatulata flore rubra* Hook.'. Secretory cavities frequently appear as transparent dots; probably occurring in all and definitely recorded in most genera. Young secretory cavities usually lined with a distinct epithelium, but the latter is soon obliterated by compression and suberization. The mode of development of the secretory cavities of *Eucalyptus globulus* has been investigated by Fohn (689). Concerning the taxonomic value of secretory cavities in *Eucalyptus*, Welch (2395) writes as follows: 'Although the distribution and number of glands is not of very great taxonomic value, yet . . . certain variations do occur and without doubt hold good throughout the distribution

of the species. Again it is quite possible to recognize certain differences in their arrangement which would permit of a rough classification into groups. . . .

AXIS

YOUNG STEM (Fig. 139 E, G, I)

Stems, when sufficiently young, frequently provided with wings, e.g. in *Eucalyptus globulus* Labill. (Fig. 139 E) and *Pimenta officinalis* Lindl. Position of origin of the **cork** somewhat variable according to the species, arising superficially in *Eugenia caryophyllus* (Spreng.) Sprague (syn. *E. caryophyllata* Thunb.) and *E. jambos* Linn., but more deep-seated (usually pericyclic) in certain other species of *Eugenia* as well as in species of *Feijoa*, *Leptospermum*, *Melaleuca* (arising in the inner part of the cortex but externally to the pericyclic fibres in *M. leucadendron* Linn.), *Myrtus*, *Pimenta*, *Psidium* (sometimes in the centre of the cortex), represented in the Kew slide collection; first-formed phellogen sub-epidermal in *Callistemon citrinus* Skeels but a second one observed to arise later in the pericycle of the same species. Cork usually stratified, being composed of layers of radially elongated thin-walled cells alternating with radially flattened cells sclerosed on their inner or outer tangential walls. Spongy cork, composed of cubical cells with delicate walls, occasionally to be found in *Eucalyptus* and *Syzygium*. **Cortex** containing stone cells in species of *Eucalyptus*, *Eugenia*, and *Metrosideros*. **Pericycle** generally including a sub-continuous ring of fibres. Secondary **phloem** usually consisting of alternating layers of fibrous and soft tissue except sometimes in *Chamaelaucium*, *Darwinia*, *Myrtus*, *Verticordia* where little or no sclerenchyma has been recorded in this position. Stone cells, often very large, present in the phloem of a few species of *Eucalyptus* and *Syzygium*. Phloem and **xylem** generally in the form of continuous cylinders traversed by narrow rays. Vessels with simple perforations. **Bicollateral vascular bundles** recorded in *Actinodium*, *Callistemon*, *Calycolpus*, *Calythrix*, *Chamaelaucium*, *Darwinia*, *Eucalyptus*, *Eugenia*, *Leptospermum*, *Melaleuca*, *Metrosideros*, *Myrcia*, *Myrrhinium*, *Myrtus*, *Psidium*, *Thryptomene*, *Tristania*, *Verticordia*, and probably occurring in other genera as well. Where the xylem is continuous, **intraxylary phloem** occurs throughout the family. Both solitary and clustered **crystals** occur, often abundantly, in the unligified tissues; solitary types sometimes situated in chambered fibres in species of *Callistemon*, *Eucalyptus*, *Melaleuca*; clustered forms present in similar fibres in species of *Eugenia*, *Myrtus*, *Syzygium*. **Secretory elements**. Tanniniferous cells abundant. Cavities containing various chemical substances, generally of an oily nature, occur in the unligified tissues, especially the cortex, of most of the species examined; observed also in the wings, e.g. in *Eucalyptus globulus* and *Pimenta officinalis*. Fourment and Melis (702) record the existence of 4 secretory canals in the pith of *Eucalyptus maculata* var. *citriodora* Hook. and *E. ficifolia* F. v. M. but not in 29 other species of *Eucalyptus*, and nodules containing secretory cavities, similar to those on the leaf, on the very young stem of '*E. spatulata flore rubra* Hook.'. According to Welch (2395) a transparent elastic substance resembling **rubber** is secreted from papillose epidermal cells on the young shoots of certain species of the *Corymbosae* group of Eucalypts and also of certain Angophoras, where it is thought to prevent excessive transpiration.

BARK

de Beuzeville and Welch (191) record the following facts concerning the bark of *Eucalyptus badjensis* de Beuz. et Welch: 'Oil glands very numerous, situated in loose parenchymatous tissue formed by the irregular widening of the medullary rays, chiefly arranged in groups visible to the naked eye. The phellogen is developed at intervals in the secondary phloem, producing

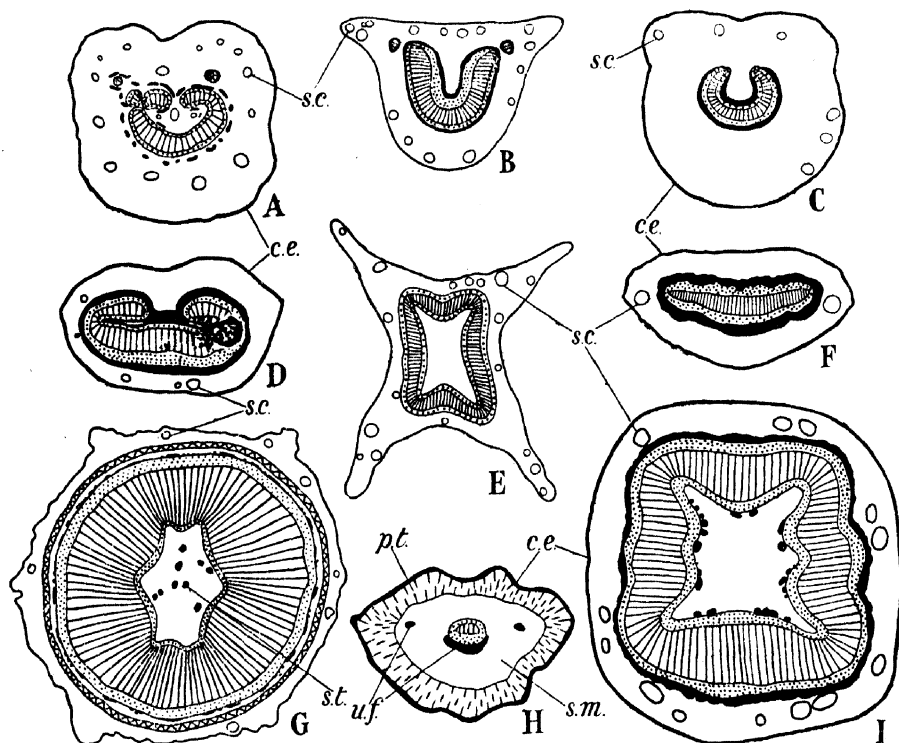


FIG. 139. MYRTACEAE

A, *Syncarpia laurifolia* Tenore. Petiole $\times 14$. B, *Eugenia caryophyllus* (Sprengel) Sprague (syn. *E. caryophyllata* Thunb.). Petiole $\times 18$. C, *Pimenta acris* Wight. Petiole $\times 19$. D, *Eucalyptus obliqua* L'Hérit. Petiole $\times 8$. E, *E. globulus* Labill. Young stem $\times 8$. F, *Callistemon citrinus* Skeels. Petiole $\times 18$. G, *Pimenta acris* Wight. Stem $\times 18$. H, *Calothamnus lateralis* Lindl. Lamina $\times 44$. I, *Eucalyptus obliqua* L'Hérit. Stem $\times 12$.

c.e. Cutinized epidermis. p.t. Palisade tissue. s.c. Secretory cavity. s.m. Spongy mesophyll. s.t. Stone cells. u.f. Unligified fibres.

a succession of absciss phelloids in the periderm.' For anatomical details concerning *Eucalyptus* bark used as a source of tannin see 'Economic Uses' on p. 629.

WOOD (Figs. 140 and 141)

Vessels typically small (less than $100\ \mu$ mean tangential diameter), very small (less than $50\ \mu$) in at least some species or specimens of *Anomomis*, *Eugenia*, *Feijoa*, *Krobia*, *Myrceugenia*, *Myrcia*, *Myrrhinum*, *Myrteckmania*, *Myrtella*, *Myrtus*, *Pimenta*, *Psidium*, and *Rhodamnia*, medium-sized (100 – $200\ \mu$) in some species of *Calycolpus*, *Campomanesia*, *Eucalyptus*,

Eugenia, *Kjellbergiodendron*, *Leptospermum*, *Marlierea*, *Melaleuca*, *Metrosideros*, *Myrcia*, *Myrtus exaltata* M. F. Bailey, *Pleurocalyptus*, *Rhodamnia*, and *Tristania*, large (more than 200 μ) in some species of *Angophora* and *Eucalyptus*; typically exclusively solitary but with occasional to numerous multiples of 2 or 3 cells in *Calyptanthus* p.p., *Eucalyptus* p.p., *Eugenia*, *Gomidesia*, *Jambosa*, *Leptospermum*, *Myrtella*, *Myrtus* p.p., and *Syzygium*, and commonly with multiples of 4 or more cells in *Angophora* (Fig. 140 H), *Eucalyptus* p.p., and *Eugenia* p.p.; the vessels usually without any definite pattern, but forming loose oblique lines in *Angophora*, *Calycorectes*, *Campomanesia*, *Eucalyptus* (Fig. 141 A and E), *Kjellbergiodendron*, *Leptospermum*, *Marlierea*, *Melaleuca*, and *Xanthostemon* and with an occasional tendency to oblique lines locally in some other genera. Vessels sometimes absent from zones separating the growth rings, such zones sometimes very conspicuous, e.g. in *Eucalyptus gigantea* Hook.; often very numerous and crowded in woods with small vessels, e.g. more than 100 per sq. mm. in some species of *Eugenia*, *Feijoa*, *Myrtus*, and *Psidium*, but sometimes with small but relatively widely spaced vessels; not more than 2–5 vessels per sq. mm. in some species of *Eucalyptus*, *Kjellbergiodendron*, *Metrosideros*, and *Rhodamnia*, 5–20 per sq. mm. in some species of *Calycolpus*, *Campomanesia*, *Eucalyptus*, *Gomidesia*, *Jambosa*, *Melaleuca*, *Myrcia*, *Psidiopsis*, *Psidium*, *Syncarpia*, *Syzygium*, and *Tristania*, 40–100 per sq. mm. in some species of *Amomis*, *Backhousia*, *Calyptanthus*, *Myrceugenia*, *Myrcia*, *Myrrhinium*, *Myrtekmania*, *Myrtella*, *Myrtus*, *Osbornia* (1649), and *Psidium*; with spiral thickening in some species of *Eugenia* and *Myrceugenia* and, according to Janssonius (1154), in *Eugenia acuminatissima* Kurz. Perforation plates simple, except in *Myrceugenia* and *Myrtus communis* L., in which they are exclusively scalariform with about 15–25 fine bars. Scalariform perforation plates also observed in a young stem of *Eugenia* sp. cultivated at Kew. Intervascular pitting typically alternate and minute, small to moderately large in *Angophora*, *Eucalyptus*, *Eugenia*, *Jambosa*, *Kjellbergiodendron*, *Osbornia* (1649), and *Tristania*, pits opposite or intermediate in *Myrceugenia* and *Myrtus communis* L.; vestured (78); pits to wood parenchyma often rare owing to presence of vasicentric tracheids, pits to ray cells usually similar to the intervacular pitting where this is small, often large, oblong and simple in the above-mentioned genera with larger intervacular pitting. Solid deposits of gum common, tyloses observed or recorded in *Angophora*, *Baeckia*, *Eucalyptus*, *Eugenia* (525), *Melaleuca*, *Rhodamnia*, *Syncarpia*, *Tristania*, and *Xanthostemon*. Mean member length 0.3–0.8 mm.

Parenchyma of 2 intergrading types, (a) predominantly apotracheal as scattered cells or irregular uniseriate bands, in most of the genera with solitary vessels (Fig. 140 K), and (b) predominantly paratracheal in the genera in which vessel multiples are relatively common; entirely or predominantly apotracheal in the following genera: *Amomis*, *Backhousia*, *Baeckia*, *Callistemon*, *Calycolpus*, *Calycorectes*, *Campomanesia*, *Decaspermum*, *Eugenia* (a few species), *Krokia*, *Leptospermum*, *Marlierea*, *Metrosideros*, *Myrceugenia*, *Myrcia*, *Myrrhinium*, *Myrtekmania*, *Myrtus* p.p., *Pimenta*, *Psidiopsis*, *Psidium*, and *Tristania*; entirely or predominantly paratracheal in the following: scanty paratracheal or vasicentric in *Eucalyptus* p.p., *Gomidesia*, and *Xanthostemon*, aliform to confluent in *Calyptanthus syzygium* (L.) Sw., *Eucalyptus* p.p., *Eugenia* p.p. (Fig. 140 E), *Kjellbergiodendron*, *Melaleuca* p.p. (together with

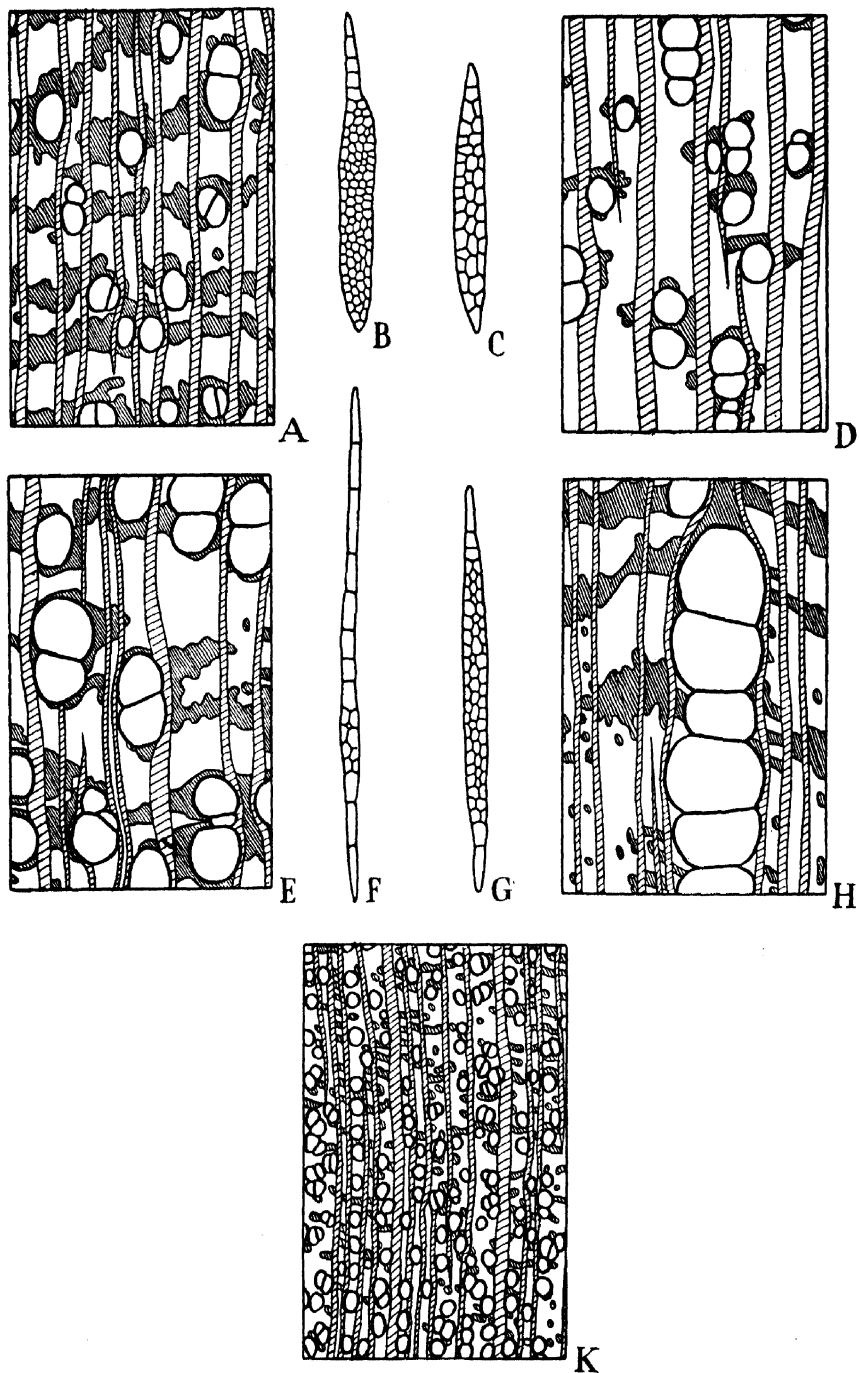


FIG. 140. MYRTACEAE

A, *Jambosa jambos* (L.) Millsp. B, *Campomanesia crenata* Berg. C, *Calypttranthes syzygium* Sw. D, *C. syzygium* Sw. E, *Eugenia urceolata* King. F, *Jambosa jambos* (L.) Millsp. G, *Decaspermum paniculatum* Kurz. H, *Angophora intermedia* DC. K, *Myrtus communis* Linn.

diffuse crystalliferous strands in addition) and *Myrtella*, the aliform parenchyma sometimes limited to the abaxial sides of the vessels (Fig. 140 D); intermediates between the 2 main types are common, e.g. diffuse and paratracheal parenchyma equally abundant in *Angophora* (Fig. 140 H) (sometimes tending to form bands), *Eucalyptus* p.p., *Melaleuca* p.p., *Osbornia* (1649), *Pleurocalyptus*, *Syncarpia*, and *Syzygium*, with broader bands of indeterminate type and often with long wings from the vessels in *Calyptranthes sericea* Grisch., *Eugenia* p.p., *Jambosa* (Fig. 140 A), *Myrtus exaltata*, *Rhodamnia* p.p., and *Syzygium cordatum* Hochst.; apparently absent from *Leptospermum javanicum* Bl. (1154); terminal bands sometimes present. Cells typically filled with a resinous or gummy substance that sometimes gives a tannin reaction; crystals comparatively rare, present in chambered cells in some species of *Angophora*, *Eucalyptus* (e.g. the Bloodwood Group), *Eugenia*, *Feijoa*, *Kjellbergiodendron*, *Marliera*, *Myrceugenia*, *Myrcia*, *Myrrhinium*, and *Psidium*. Some of the crystalliferous cells of *Myrcia* and *Psidium* are distinctly wider than those of the normal strand. Silica grains have been reported by Janssonius (1154) in *Eugenia sexangulata* Koord. et Valet. and *E. densiflora* Duthie. Strands usually of up to 8 cells. **Rays** occasionally with a suggestion of being of 2 distinct sizes; typically up to 2-3 cells wide, exclusively uniseriate or with only occasional biseriate parts in *Eucalyptus* p.p., *Melaleuca*, *Pleurocalyptus*, *Tristania* p.p., and *Xanthostemon*, 4-6 cells wide in some species of *Baeckia*, *Calyptranthes*, *Campomanesia*, *Leptospermum*, *Myrtus*, and *Rhodamnia*, up to 8 cells wide in *Gomidesia*; less than 1 mm. high except in some of the species with more than 10 marginal rows of upright cells; uniseriates numerous, typically composed of square to upright cells only, except in the woods with homogeneous rays and in *Eucalyptus*, and often only 1 or 2 cells high; composed of mixed procumbent and upright to square cells in some species of *Eugenia*, and wholly or mostly of procumbent cells in the other species of *Eugenia* and in *Eucalyptus*; mostly 13-20 rays per mm., sometimes more than 20 per mm., e.g. in *Calycorectes*, *Myrteckmania*, *Myrtus*, and *Rhodamnia*, sometimes rather fewer than 13 per mm., for example in *Angophora*, *Calycolpus*, *Calyptranthes*, *Eucalyptus*, *Eugenia*, *Leptospermum*, *Psidium*, *Syncarpia*, and *Xanthostemon* and about 3 per mm. in *Gomidesia*; typically heterogeneous (Kribs's Types II A and B) with 4-10 marginal rows of upright cells; with more than 10 rows of upright cells (often Kribs's Heterogeneous Type I), in some species of *Jambosa*, *Myrceugenia*, *Myrcia*, *Psidiopsis*, and *Rhodamnia*; with only 1-3 rows in some species of *Calyptranthes*, *Campomanesia*, *Eucalyptus*, *Feijoa*, *Gomidesia*, *Kroki*a, *Metrosideros*, *Myrtella*, and *Psidium*; homogeneous (Kribs's Type I) in *Angophora*, *Eucalyptus* p.p., e.g. *E. maculata* Hook., *Myrcia* p.p., and *Tristania* p.p.; with sheath cells in *Gomidesia*. Cells typically filled with a dark gummy or oily substance and without crystals; crystals abundant in *Calyptranthes syzygium* (L.) Sw.; silica has been reported (194, 794, 1126) in *Eugenia*, *Metrosideros*, and *Tristania*. **Fibres** typically with bordered pits, the pits varying from rather few to very numerous, usually equally distributed on both the radial and the tangential walls, but sometimes more numerous on the tangential walls; rarely more numerous on the radial walls; pits simple or with indistinct borders in *Eugenia*, *Gomidesia*, and *Jambosa*. According to Gouwentak (799) both libriform fibres and fibre-tracheids occur in

some species of *Eucalyptus*. Walls moderately to very thick. Often containing gum, oil, or other matter, which sometimes produces the appearance of septa; Gouwentak (799) notes the presence of tannin in the fibre-tracheids of *Eucalyptus rostrata* Schl. Occasional septate fibres present in some species, e.g. of *Eugenia* (1154) and *Marlierea*. Mean length 0.7–2.0 mm. **Vasicentric tracheids** present in most of the genera, not observed or not clearly distinguishable from the fibre-tracheids in some species of *Backhousia*, *Baeckia*, *Decaspermum*, *Eucalyptus*, *Gomidesia*, *Jambosa*, *Krobia*, *Myrceugenia*, *Myrtus*, *Psidium*, *Syncarpia*, *Syzygium*, and *Xanthostemon*. **Intercellular canals** of

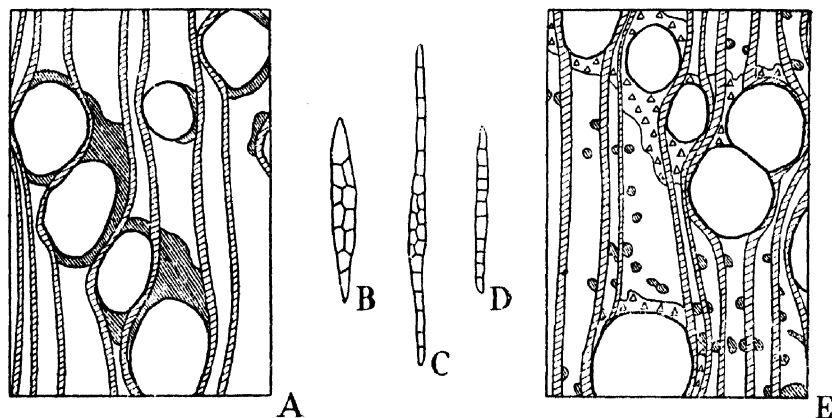


FIG. 141. MYRTACEAE

A, *Eucalyptus globulus* Labill. B, *E. resinifera* Sm. C, *E. regnans* F. Muell. D, *E. gigantea* Det. E, *E. marginata* Sm.

the vertical traumatic type reported (1851) to occur in *Angophora*, *Eucalyptus*, and *Rhodamnia*, those of *Eucalyptus* sometimes very large; their origin is discussed by Jacobs (1136); radial schizogenous canals recorded by Janssonius in the rays of *Eugenia cuprea* Koord. et Valet., and *Leptospermum javanicum* Bl. **Growth rings.** The seasonal development of the wood in *Eugenia* and *Psidium* has been investigated by Coster (481) and Chowdhury (414). The nature of the **ash** has been used as an aid to distinguishing between species of *Eucalyptus* (337, 338, 518, 522, 523). The effect of water-supply on the structure of the wood and the rate of water conduction in *Eucalyptus rostrata* Schlecht. has been investigated by Greiss (816–17).

ROOT

Musson and Carne (1576) have recorded the normal occurrence of adventitious roots on the trunk of *Melaleuca linariifolia* Sm. Bird (199) describes the cortex of the climbing roots of *Metrosideros hypericifolia* A. Cunn. as composed of chlorophyllous cells when young, but becoming lignified and serving as mechanical tissue when older. Other features recorded in the same species include the normal absence of root hairs except when their formation is induced by treatment in a moist chamber; the conspicuous endodermis; the vessels in the xylem of the central cylinder with small lumina and very thick

walls. The vessels in the absorbing roots are rather larger and the cortex does not become converted to mechanical tissue.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The Myrtaceae, as understood by Bentham and Hooker, included the Lecythidaceae, now generally treated as a separate family. Comparison of the anatomical features of the Lecythidaceae with those of the Myrtaceae *sensu stricto* shows that there are important differences between the two groups, and favours their recognition as distinct families.

(ii) FROM WOOD STRUCTURE

There do not appear to be any consistent differences between the Myrteae and the Leptospermoideae. Differences between species of the same genus are sometimes unusually marked, e.g. between *Calypttranthes sericea* Griseb. and *C. syzygium* (L.) Sw., *Myrcia* spp., and *Myrtus communis* L. and *M. exaltata* M. F. Bailey, the latter suggesting *Eugenia*. *Gomidesia lindeniana* Berg. is distinct in some respects. For comparison with Lecythidaceae see that family. Dadswell and Ingle (531) state that the wood structure definitely supports the revision of the genus *Eugenia* proposed by Merrill and Perry, and that, anatomically, the species of the New World belonging to the genus *Eugenia* are quite distinct from the majority of the Australian and New Guinea species. They, however, consider that the two Australian species *Eugenia carissoides* F. Muell. and *E. macrophylla* C. T. White et Francis are true *Eugenias*, similar to those of the New World. On the other hand, these authors have found little to support the reinstatement of the genera *Acmena* and *Cleistocalyx*.

ECONOMIC USES

Essential oils are distilled from the flowers and foliage of various members of the family. The well-known Eucalyptus oil used in medicine is said to be derived from *Eucalyptus polybracteata* R. T. Baker, *E. dumosa* A. Cunn., and other species of *Eucalyptus*. Lemon-scented Eucalyptus oil is obtained from *E. maculata* var. *citriodora* Hook., whilst the oil of *E. dives* Schau. is used in the manufacture of thymol. Cajuput oil, also used in medicine, is derived from *Melaleuca leucadendron* Linn. and other species of *Melaleuca*. Other important products derived from the family include Cloves (*Eugenia caryophyllus* (Sprengel) Sprague syn. *E. caryophyllata* Thunb.), Allspice (*Pimenta officinalis* Lindl.); Guava Fruits (*Psidium guajava* Linn.), Rose Apple (*Eugenia jambos* Linn.), and Jambolana Fruits (*E. jambolana* Lam.). The bark of various species of *Eucalyptus* has been used as a source of tannin, and at one time Mallet Bark (*Eucalyptus occidentalis* Endl.) was imported into European countries from Western Australia for use in tanning. According to Wiesner (2423) true Mallet Bark may be distinguished from that of other species of *Eucalyptus* by the horny transverse fracture. Transverse surfaces of mature specimens exhibit 1 or more layers of cavities filled with dark red, glistening masses of Eucalyptus Kino. Commercial samples consist mostly of the inner bark. The phloem parenchyma and rays which are 2-3 cells wide consist of thin-walled, tanniniferous parenchyma. Small or large clusters of radially

arranged groups of fibres occur in the secondary phloem. Paired crystals of calcium oxalate are characteristic of this as well as of other *Eucalyptus* barks. Further particulars concerning mallet bark have been recorded by Bodenstab (211). The many important timbers produced by this family almost all belong to the sub-family Leptospermoideae and are mostly species of the single genus *Eucalyptus*. Among the best known are Jarrah (*Eucalyptus marginata* Sm.), Karri (*E. diversicolor* F. Muell.), and 'Tasmanian Oak' (*E. gigantea* Hook. f., *E. obliqua* L'Hérit., and *E. regnans* F. Muell.). Many other species are well known at least locally, e.g. Tallow wood *E. microcorys* F. Muell. and the various 'Ashes', 'Boxes', Ironbarks, and Gums.

Two closely related species of *Metrosideros*, Kajoe Lara and Kajoe Nani from the Netherlands East Indies, are reputed to be specially suited for marine construction, the high silica content making them resistant to marine borers (1126), and the same appears to be true of the Australian Turpentine, *Syncarpia laurifolia* Ten. The Brush Box, *Tristania conferta* R. Br., and Satinay, *Syncarpia billii* Bailey, are important construction timbers in Australia and species of *Eugenia* are used for building in Burma, India, and tropical and sub-tropical America. Many of the other genera produce hard, tough timbers that are used locally and the woods of the family as a whole are excellent for fuel.

Many species are extensively grown as exotics in forestry plantations in different parts of the world, e.g. *Eucalyptus globulus* Labill., *E. maculata* Hook., *E. microcorys* F. Muell., *E. robusta* Sm., *E. rostrata* Schlecht., and *E. saligna* Sm.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Actinodium, Angophora, Beaufortia, Callistemon,* Calothamnus, Calycolpus, Calycorectes, Calyptranthos, Calytrix, Campomanesia, Chamaelaucium, Cupheanthus, Darwinia, Decaspermum, Eremaea, Eucalyptus,* Eugenia,* Feijoa,* Gaslondia, Jambosa, Kunzea, Leptospermum,* Lhotzkya, Marlierea, Melaleuca,* Metrosideros, Myrcia, Myrtus,* Pileanthus, Pimenta,* Psidiopsis, Psidium,* Regelia, Rhodamnea, Rhodomyrtus, Syncarpia,* Syzygium, Thryptomene, Tristania, Verticordia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Anomis, Angophora, Backhousia, Baeckia, Callistemon, Calycolpus, Calycorectes, Calyptranthos, Campomanesia, Decaspermum, Eucalyptus, Eugenia, Gomidesia, Jambosa, Kjellbergiodendron, Krokia, Leptospermum, Marlierea, Melaleuca, Metrosideros, Myrceugenia, Myrcia, Myrrhinium, Myrtekmania, Myrtella, Myrtus, (Osbornia), Pimenta, Pleurocalyptus, Psidiopsis, Psidium, Rhodamnia, Syncarpia, Syzygium, Tristania, Xanthostemon.

LITERATURE

(i) On General Anatomy

Baker and Smith 107-11, Bandulka 132, de Beuzeville and Welch 191, Bird 199, Bodenstab 211, Boer 214, Brogli 277, Fohn 689, Fourment and Melis 702, Johnson 1185, Motte 1566, Musson and Carne 1576, Ohtani 1636, Wallis and Santra 2535, Welch 2395, Wiesner 2423.

(ii) *On Wood Structure*

Anonymous 27, Bailey 73, 78, Baker 104, Beekman 167, Benoist 170, den Berger 179, 182, Besson 186, Betts, M. W. 188-9, Bianchi 194, Brown, F. B. H. 282, Burgerstein 310, 312, Campion 337, 338, Chowdhury 411, 414, Coster 481, Dadswell *et al.* 518, 522, 523, 525, 531, Diehl 582, Foxworthy 705, Garratt 744, Giordano 786, Gonggrijp 794, Gouwentak 799, Greguss 2522, Greiss 816, 817, Howard 1088, van Iterson 1126, Jacobs 1136, Janssonius 1154, Jolly 1188, Jones 1191, Kanehira 1206, 1209, Kribs 1283, Lecomte 1334, McNair, J. B. 1476, Milanez 1521, Panshin 1649, Pearson and Brown 1679, Pereira 1687, Record 1780, 1783, 1801, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2207, Tupper 2294, Webber 2377, Welch 2398, 2402, 2403, 2406, Williams 2430.

137. LECYTHIDACEAE

(FIG. 142 on p. 634; FIG. 143 on p. 638)

SUMMARY

(i) GENERAL

A tropical family of trees and shrubs which differs from the Myrtaceae in the absence of **secretory cavities** from the leaves and ground tissues of the stem. **Intraxylary phloem** is also absent. The leaf is usually dorsiventral, or, more rarely, centric. The **stomata** are usually confined to the lower surface of the leaf, but sometimes occur on the upper side as well. They are usually cruciferous. The structure of the **petiole**, which is frequently somewhat complex, provides useful diagnostic characters. The presence of **cortical vascular bundles** is one of the most characteristic features of the axis. These appear to be truly cauline, since they have been seen to be accompanied by separate leaf trace bundles in certain species.

(ii) WOOD

Vessels very small to large, sometimes with pronounced radial multiples or irregular clusters, perforations simple, intervacular pitting alternate and minute to large, pits to parenchyma often large and simple, members of medium length. **Parenchyma** typically in apotracheal bands, varying from uniseriate and broken to wide and continuous, but predominantly aliform to confluent in a few genera, long, chambered, crystalliferous strands characteristic of the New World genera. **Rays** mostly 2-3 cells wide, but very broad in some genera, distinctly heterogeneous to homogeneous. **Fibres** with simple pits, of medium length to very long. **Intercellular canals** of the vertical traumatic type present in some genera.

LEAF

Usually dorsiventral; centric structure recorded in certain species of *Asteranthos* and *Foetidia*. **Hairs** simple, unicellular or uniseriate, occasionally tending to be tufted. **Glands** present on the lower side at the base of the leaf in *Napoleona*. Lower **epidermis** papillose in certain species of *Couratari* and *Lecythis*. **Stomata** usually confined to the lower surface, but occurring on the upper side also in a few species of *Barringtonia*, *Foetidia*, *Gustavia*; generally cruciferous, but reported to be rubiaceous in *Chytroma idatimon* Miers. Ordinary stomata are accompanied by especially large ones in *Napoleona whitfieldii* Decne. **Hypoderm** recorded below the upper epidermis

in a few species of *Barringtonia* and *Foetidia*. **Mesophyll** stated to contain sclerenchymatous fibres in *Asteranthos*. **Petiole**. Transverse sections through the distal end in the few species examined exhibit a main arc of widely spaced collateral bundles, sometimes accompanied by accessory strands on the adaxial side, e.g. in species of *Bertholletia*, *Gustavia* (Fig. 143 E), *Lecythis*, and on the abaxial side as well in *Gustavia*. Solereder records the occurrence in the petiole of a single arc of 5 bundles in the Napoleoneae, and 2 or 3 concentrically arranged arcs in the Barringtonieae and Lecythideae. A petiole of *Napoleona imperialis* Beauv. examined at Kew is shown in Fig. 143 H.

Crystals, according to Solereder, solitary in the Napoleoneae; mixed solitary and clustered in the Lecythideae; star-shaped clusters in the Barringtonieae. **Secretory elements**. Cells containing tannin usually present. Secretory cavities absent.

AXIS

YOUNG STEM (Fig. 143 J-K)

Cortical vascular bundles occur in *Asteranthos*, *Barringtonia*, *Bertholletia* (Fig. 143 J), *Careya*, *Couratari*, *Foetidia*, *Gustavia*, *Lecythis*, *Napoleona* (Fig. 143 K), *Planchonia*; said to be inversely orientated in *Barringtonia*, *Foetidia*, *Gustavia*, *Planchonia*; normally orientated in other genera. Smaller cortical bundles tending to be centric. Cortical bundles of genera represented in the Kew slide collection sheathed by thick-walled fibres accompanied, at the outer periphery, by a single layer of cells containing solitary crystals, except in *Gustavia* where cluster crystals occur in the corresponding position. According to Solereder the number of cortical bundles in the Napoleoneae is much smaller than in the remainder of the family. **Cork** arising superficially, usually composed of flattened cells, sometimes stratified into layers with thin cell walls alternating with others having the inner or outer tangential wall thickened in species of *Cariniana*, *Gustavia*, *Lecythopsis*. **Pericycle** containing a somewhat interrupted ring of fibres in all of the few species represented in the Kew slide collection, but the fibre strands become more widely spaced as the stems grow older. Secondary **phloem** generally stratified into fibrous and soft portions. Phloem and **xylem** usually in the form of continuous cylinders traversed by narrow rays, but rays broader and provided with enlarged, triangular, distal ends in *Napoleona* (Fig. 143 K). Vessels with simple perforations; scalariform plates also recorded (see 'Wood'). Primary phloem strands in the last genus also triangular with outwardly directed apices. **Intraxylary phloem** absent. **Secretory elements**. Mucilage canals recorded in species of *Bertholletia*, *Couratari*, *Eschweilera*, *Lecythis*, but apparently not present throughout these genera. Cells with amorphous, probably tanniniferous contents common in the unligified tissues. Solitary and clustered **crystals** common (see also under 'Cortical Bundles').

WOOD (Fig. 142)

Vessels mostly medium-sized (100–200 μ mean tangential diameter), moderately small (50–100 μ) in *Asteranthos* p.p. (582), *Careya* p.p. (582), *Eschweilera*, *Foetidia*, *Gustavia*, and *Napoleona*, very small (25–50 μ) in *Grias*, large (more than 200 μ) in *Bertholletia*, *Cariniana*, *Couratari*, and *Couroupita*; solitary and in small multiples, commonly with multiples of 4 or

more cells in *Careya*, *Eschweilera* p.p., and *Lecythis* p.p., with irregular clusters in *Allantoma*, *Careya*, and *Napoleona*; very variable in number, ranging from 1.5–5 per sq. mm. in *Careya*, *Cariniana*, *Couroupita*, *Eschweilera*, and *Lecythis* to 20–40 in *Foetidia*, *Grias*, and *Gustavia*, the latter sometimes with more than 40 per sq. mm. (582); spiral thickening recorded by Janssonius (1154) in *Planchonia undata* Bl. Perforation plates simple, except for occasional scalariform or reticulate plates observed in *Allantoma* and one specimen of *Barringtonia speciosa* L. and reported by Record and Hess (1886) in *Asteranthos* and *Grias*. Intervascular pitting alternate, except in *Grias*, in which it is transitional between scalariform and opposite; varying in size from minute, e.g. in *Eschweilera*, *Foetidia*, *Grias*, and *Gustavia*, to large, e.g. in *Barringtonia*, *Combretodendron*, *Couroupita*, and *Petersianthus*; sometimes with occasional pits elongated horizontally to about twice their usual width, e.g. in *Planchonia andamanica* King and some species of *Napoleona* (582); pits to ray and wood parenchyma typically including many large, elongated, slightly bordered or simple pits, such pits tending to be circular in woods with minute intervacular pitting, e.g. in *Gustavia*, particularly when adjoining ray cells; absent from *Chytroma*. Tyloses observed in *Allantoma*, *Asteranthos*, *Bertholletia*, *Careya*, *Cariniana*, *Chydenanthus*, *Combretodendron*, *Couratari*, and *Lecythis*; sclerosed, according to Diehl (582), in some specimens of *Asteranthos*, *Eschweilera*, and *Lecythis*; solid deposits common in *Foetidia mauritiana* Lam. Mean member length 0.4–0.6 mm. **Parenchyma** typically abundant and apotracheal banded with some paratracheal; in numerous, short, irregular (almost diffuse) lines in *Asteranthos*, *Barringtonia* (with vasicentric or aliform parenchyma in addition and sometimes predominant, see Fig. 142 A) and *Grias* (1894); in continuous bands 1, occasionally 2, cells wide in *Careya*, *Cariniana* (Fig. 142 D), *Couratari*, *Couroupita*, *Eschweilera* p.p., *Foetidia*, *Gustavia* (Fig. 142 H), *Lecythis* p.p., and *Napoleona*, in broader bands in *Allantoma*, *Bertholletia*, *Eschweilera* p.p., and *Lecythis* p.p.; the fine bands sometimes very numerous, e.g. 25 or more per mm. in *Gustavia rhodantha* Standl. and *Napoleona parviflora* Bak. f.; predominantly paratracheal, aliform to confluent and usually with some diffuse, in *Chytroma*, *Combretodendron* (Fig. 142 E), *Petersia* (582), and *Petersianthus*; parenchyma very scarce or absent from the only available specimen of *Grias fendleri* Seem. Crystalliferous strands are common in the New World genera and, according to Diehl (582), serve as a basis for separating these from the rest of the family, with the exception of *Foetidia*. The crystalliferous cells often occupy the complete length of the strand and are sometimes locally biseriate (tangential section), e.g. in *Cariniana*; the strands occur on the margins of the apotracheal bands, except in *Foetidia*, in which they are scattered among the fibres. The ordinary strands are most commonly of up to 6 or 8 cells. **Rays** very variable in width, ranging from exclusively uniseriate in occasional specimens of *Eschweilera* and *Lecythis* to up to 20 cells wide in *Napoleona vogelii* Hook. et Planch.; mostly up to 2–3 cells wide; 4–10 cells wide in *Barringtonia*, *Bertholletia*, *Chydenanthus*, *Combretodendron*, *Couroupita*, *Gustavia* p.p., and *Petersianthus*, more than 10 cells wide in *Grias*, *Gustavia* p.p., and *Napoleona*; typically more than 1, and often several, millimetres high, but less than 1 mm. in *Allantoma*, *Eschweilera*, *Foetidia*, *Lecythis* p.p., *Petersianthus*, and *Planchonia*; uniseriate rays sometimes very

scarce or absent, e.g. in *Barringtonia* p.p., *Careya*, *Cariniana*, *Combretodendron*, *Couroupita*, *Grias*, *Lecythis* p.p., and *Napoleona*, when present usually composed of mixed procumbent and upright cells; mostly 5–12 rays per mm., more numerous (up to 16 per mm.) in some species of *Eschweilera*, *Foetidia*, and *Planchonia*, fewest (1–3 per mm.) in *Grias* and *Napoleona*;

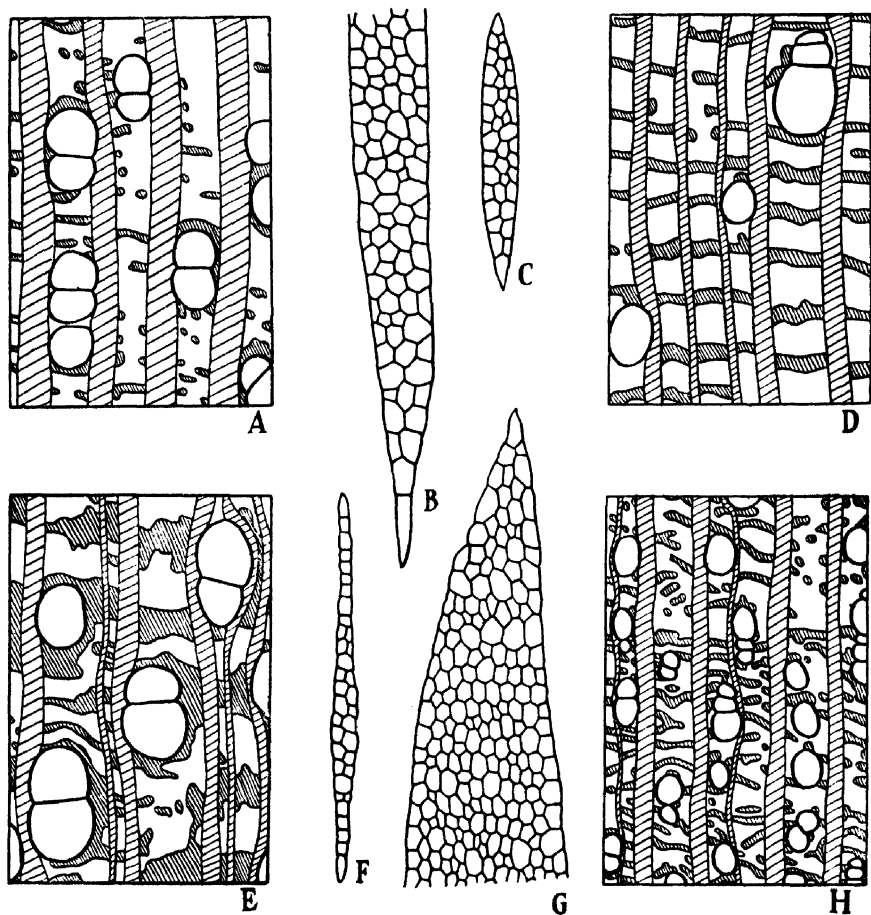


FIG. 142. LECYTHIDACEAE

A, *Barringtonia acutangula* (L.) Gaertn. B, *B. acutangula* (L.) Gaertn. C, *Cariniana estrellensis* (Raddi) Kuntze. D, *C. estrellensis* (Raddi) Kuntze. E, *Combretodendron africanum* Exell. F, *Eschweilera calyculata* Pittier. G, *Napoleona vogelii* Hook. et Planch. H, *Gustavia brasiliiana* DC.

commonly almost homogeneous, with 1 or 2 marginal rows of square cells present in some of the rays, homogeneous (Kribs's Types I and II) in *Allantoma*, *Cariniana*, *Couratari*, *Eschweilera*, *Lecythis*, and *Napoleona* p.p., distinctly heterogeneous (Kribs's Type II, mostly A, occasionally B), in *Asteranthos*, *Barringtonia* p.p., *Careya*, *Combretodendron*, *Foetidia*, *Gustavia*, *Petersianthus*, and *Planchonia*; the cells are nearly all almost square in *Asteranthos* (1886); in *Gustavia brasiliiana* DC. small groups of procumbent cells alternate with square or upright cells; sheath cells occasionally present

in some species of *Barringtonia*. Gummy deposits common, often filling the cells; crystals observed or reported in some species of *Barringtonia*, *Cariniana*, *Chydenanthus*, *Couroupita*, *Gustavia*, and *Napoleona*, and, according to Diehl (582), more common in the Old than in the New World genera. Inclusions of silica present in the ray cells of *Eschweilera longipes* Miers (1126). **Fibres** typically with simple pits, but the pits distinctly bordered in *Allantoma*, and with small, indistinct borders in a few genera, e.g. *Couroupita* and *Petersianthus*; the pits more numerous on the radial than on the tangential walls. Typically with thick to very thick walls, sometimes with a gelatinous layer, e.g. in *Barringtonia*, *Grias*, *Gustavia*, and *Petersia* (582); walls moderately thin in some species of *Bertholletia*, *Cariniana*, *Couratari*, *Couroupita*, and *Grias*. Diehl (582) reports septate fibres in *Planchonia andamanica* King. Mean length 1.0–2.4 mm. **Intercellular canals** of the vertical traumatic type, similar to the gum veins of *Eucalyptus*, reported by Record and Hess (1886) in several specimens of *Eschweilera*, a few of *Lecythis*, and one of *Cariniana*.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

The absence of secretory cavities and intraxylary phloem, the presence of cortical bundles in the axis, and the frequently complex vascular structure of the petiole serve to differentiate the Lecythidaceae from the Myrtaceae.

(ii) FROM WOOD STRUCTURE

Diehl (582) has made a study of this family and comes to the following conclusions:

‘Excepting the occurrence of crystal strands, differences within the family, i.e. between genera and groups of genera, are few, and, being of degree rather than of kind, are at present of dubious diagnostic value.’

‘The Lecythidaceae may be separated into two sections on the basis of the presence or absence of crystal strands. These structures are a unique and distinctive character and show a striking correlation with geographical distribution, being absent in the Old World genera, except *Foetidia*, and constantly present in those of the New World.’

‘The anatomical structure of the Lecythidaceae lends support to their segregation from the Myrtaceae.’

‘On the basis of the anatomical structure, *Asteranthos* and *Napoleona* are properly included with the Lecythidaceae.’

‘The Myrtaceae differ from the Lecythidaceae principally in having mostly solitary pores, fibres with distinctly bordered pits, and wood parenchyma that is paratracheal or diffuse instead of distinctly metatracheal.’

It should be pointed out, however, that the parenchyma distinction is not as clear as Diehl implies. For example, in the author’s opinion, the parenchyma of *Chytroma* (not included by Diehl) should be classified as aliform and that of *Combretodendron* and *Petersianthus* as predominantly paratracheal (aliform to confluent); also the apotracheal parenchyma of *Barringtonia* p.p. and *Planchonia* is as much diffuse (as opposed to metatracheal) as in some genera of Myrtaceae; the Myrtaceae also include some genera with predominantly paratracheal parenchyma, e.g. *Gomidesia*, *Kjellbergiodendron*, and *Melaleuca*.

ECONOMIC USES

The hard, lidded capsules of *Lecythis* are known as Monkey Pots and used in South America as water vessels after removal of the seeds. The most familiar product in European countries is the Brazil nut (*Bertholletia excelsa* H. B. et K.). Sapucaia nuts (*Lecythis usitata* Miers and *L. ollaria* Linn.) are less well known. The Anchovy Pear is the fruit of *Grias cauliflora* Linn.

The Surinam timber Manbarklak, *Eschweilera longipes* Miers and *E. subglandulosa* (Steud.) Miers, is remarkable for being more resistant to marine borers even than Demarara Greenheart, owing to the presence of silica particles (1126). It is reputed to be becoming of increasing importance for marine construction, particularly in brackish water (1886).

The timber of *Cariniana pyriformis* Miers has been exported from Colombia to Europe and the U.S.A. under the name Colombian Mahogany. Silica, which is likewise present in this timber, is stated by Record and Hess (1886) to cause excessive dulling of tools when the wood is being worked.

Some other timbers from this family are used locally for general utility purposes and Record and Hess consider that the American members are likely to become important owing to their abundance, large dimensions, and good form, and the wide range of properties among the different species. Pearson and Brown (1679) include *Barringtonia acutangula* Gaertn. and *Careya arborea* Roxb. as timber species in India.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Asteranthos, Barringtonia, Bertholletia,* Careya, Cariniana, Couratari, Eschweilera, Foetidia, Gustavia,* Lecythis,* Lecythopsis, Napoleona,* Petersia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Allantoma, Asteranthos, Barringtonia, Bertholletia, Careya, Cariniana, Chydenanthus, Chytroma, Combretodendron, Couratari, Couroupita, Eschweilera, Foetidia, Grias, Gustavia, Lecythis, Napoleona, (Petersia), Petersianthus, Planchonia.

LITERATURE

(i) On General Anatomy

Knuth 1257.

(ii) On Wood Structure

Benoist 170, den Berger 179, Cooper and Record 461, Dadswell and Record 533, Desch 574, Diehl 582, Dixon 592, Howard 1088, van Iterson 1126, 1127, Knuth 1257, Kribs 1283, Martin-Levigne 1450, Pearson and Brown 1679, Pfeiffer, J. Ph. 1713, Record 1802, 1836, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Stone 2202, 2207, Sudworth and Mell 2219, Tupper 2295, Williams 2430.

138. MELASTOMACEAE

(FIG. 138 on p. 622; FIG. 143 on p. 638; FIG. 144 on p. 640; FIG. 145 on p. 646)

SUMMARY

(i) GENERAL

A mainly tropical family of herbs, shrubs, and trees. Some species, e.g. of *Medinilla*, are epiphytes. Various complex types of **hairs**, which may be glandular or non-glandular, occur very widely and constitute a characteristic feature. Simple hairs are relatively infrequent. A great many details concerning their more particular structure and distribution, given by Solereder, have not been repeated here, but they would be an aid to the identification of genera and species if reinvestigated. The **stomata** are usually ranunculaceous or cruciferous, but caryophyllaceous and, more rarely, rubiaceus types have been recorded. Stomata are occasionally almost entirely surrounded by a single cell, and sometimes confined to cavities of various sizes. The **petiole**, in transverse sections of all investigated species, exhibits an arc composed of widely spaced vascular bundles which are frequently accompanied by variously arranged accessory bundles. In the **stem**, the outstanding features are the universal occurrence of **intraxylary phloem**, and the common, but not universal, occurrence of **cortical** and **medullary bundles** which may be present alone or together in different genera and species. **Interxylary phloem** also occurs in a number of genera. **Cork** arises superficially in most genera, or in the pericycle in others. It is occasionally replaced by **aerenchyma** in submerged parts of a few aquatic species. The **endodermis** is usually well defined, but the **pericycle** never contains a composite and continuous ring of sclerenchyma, although a proportion of sclerosed cells is often present.

(ii) WOOD

Vessels usually small, occasionally medium-sized, small multiples and clusters common, perforations simple, intervacular pitting typically alternate, commonly minute, but sometimes moderately large, vested, pits to parenchyma either similar to the intervacular pitting or conspicuously elongated and simple; members of medium length. **Parenchyma** typically paratracheal only and rather sparse, particularly in the Melastomoideae, but varying from aliform to broad apotracheal bands in a few genera; sometimes in isolated groups among the fibres and characterized by conspicuous intercellular spaces; paratracheal parenchyma always present. **Rays** of the Melastomoideae typically uniseriate and composed almost entirely of square or upright cells; 2-4 cells wide in a few species. Rays of the Astronioideae and Memecyleae typically 2-5 cells wide, the larger rays composed mainly of procumbent cells with 1-3 marginal rows of upright cells, the uniseriate rays often very low; wholly uniseriate in a few species, composed mainly of procumbent cells. **Fibres** of the Astronioideae and Memecyleae typically with bordered pits and thick walls; those of the Melastomoideae with simple pits, usually septate and with thin walls, commonly in distinct radial rows; often with parenchyma-like patches or bands of thinner-walled cells with

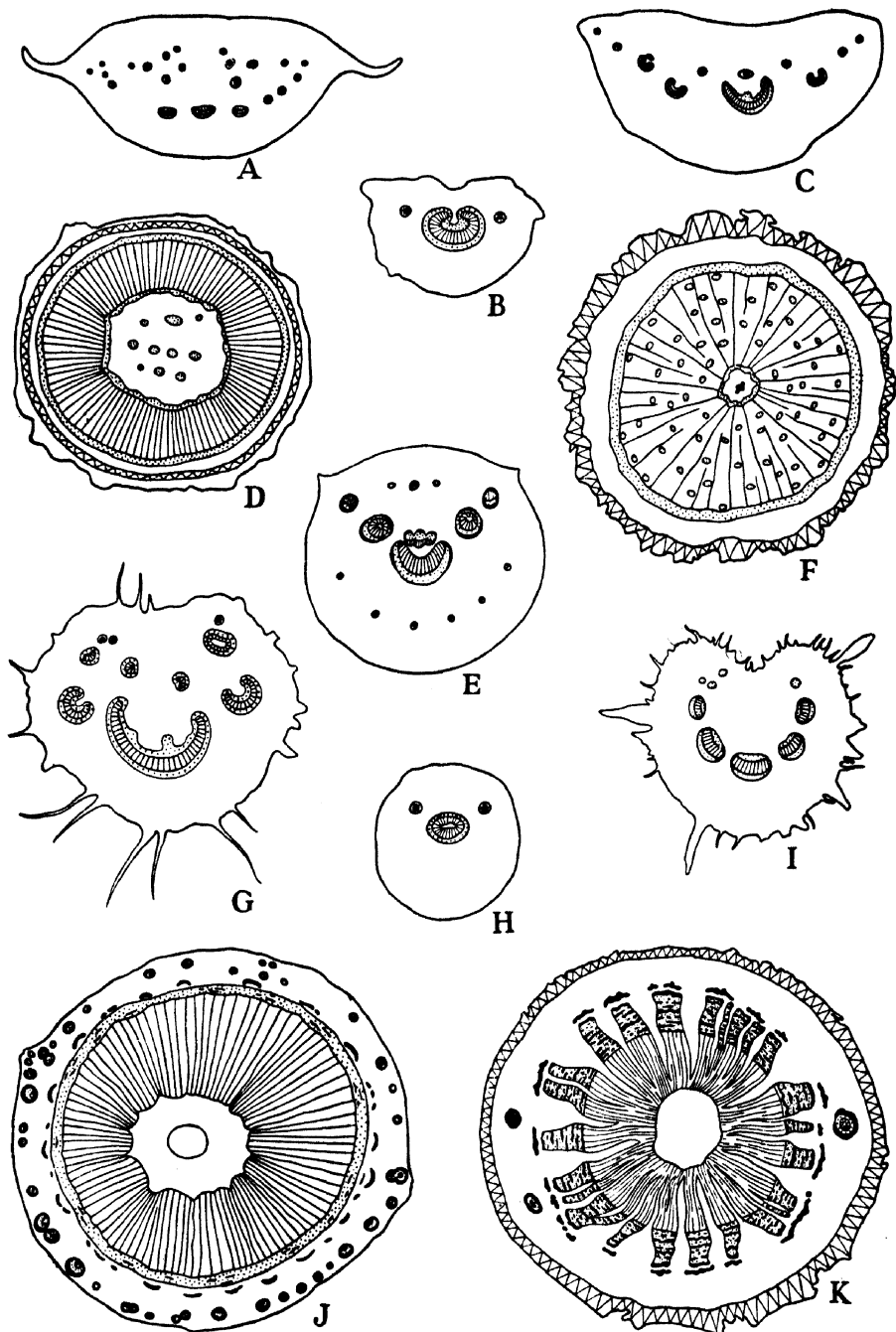


FIG. 143. MELASTOMACEAE, A-D, F-G, and I; LECYTHIDACEAE, E, H, and J-K

A, *Medinilla magnifica* Lindl. Petiole $\times 4$. B, *Memecylon umbellatum* Kostel. Petiole $\times 13$. C, *Centradenia grandifolia* Endl. Petiole $\times 13$. D, *Melastoma normale* D. Don. Stem $\times 15$. E, *Gustavia speciosa* DC. Petiole $\times 8$. F, *Memecylon umbellatum* Kostel. Stem $\times 18$. G, *Tibouchina semidecandra* Cogn. Petiole $\times 19$. H, *Napoleona imperialis* Beauv. Petiole $\times 8$. I, *Bredia hirsuta* Blume. Petiole $\times 15$. J, *Bertholletia excelsa* Humb. et Bonpl. Stem $\times 13$. K, *Napoleona imperialis* Beauv. Stem $\times 17$.

conspicuous intercellular spaces; very short to moderately long. **Included phloem** of the 'foraminate' type present in 6 genera of the Astronioideae and Memecyleae.

LEAF

Dorsiventral or centric; glabrous or hairy. **Hairs** (Fig. 144) consisting for the most part of somewhat variable and complex types, such as those mentioned below, but these and other modifications also occur in many other genera besides those mentioned by name. The more complex hairs are often partly or wholly sclerenchymatous or even contain vascular bundles. The relatively simple types described below under (i) and (ii) are comparatively rare. Glandular hairs widely distributed.

A. *Non-glandular*. (i) Unicellular or resembling papillae in species of *Kibessia*, *Macairea*, *Marcetia*, *Miconia*. (ii) Uni- or biseriate, with thick walls and I-shaped lumina in *Trembleya* sp.; other uniseriate types recorded in *Sonerila* and *Vepricella*. (iii) With multiseriate stalks and terminal cells arranged like the hairs of a paint-brush in *Tococa* sp. (Fig. 144 B). (iv) Candelabra hairs in *Dichaetanthera*, *Dissochaeta*, *Dissotis*, *Kibessia*, *Marumia*, *Medinilla* (Fig. 144 D), *Meriania*, *Omphalopus*. (v) Stellate, with short stalks in *Miconia* sp. (vi) Peltate in *Astronia*. (vii) Shaggy hairs as in Fig. 144 E, I, and K.

B. *Glandular*. (i) Shaggy hairs, resembling some of the non-glandular types described above, but with multicellular, glandular heads, e.g. in *Pyramia* (Fig. 144 C). (ii) Small, with well-defined, multicellular, variously shaped heads. (iii) Bladder-like glands, resembling those of the Labiatae, in *Blastus*, *Chaetostoma*, *Lavoisiera*, *Macairea*, *Microlicia*, *Trembleya*.

According to de Cordemoy (468) the **emergences** on the trees and shrubs belonging to the Osbeckieae consist of epidermal and cortical tissue, the epidermis of the emergences being smooth in some but provided with conical papillae in other species of *Dichaetanthera*. Cortical tissue of the emergences often more or less lignified. Transitions between emergences and true hairs also occur, e.g. in *Tristania*.

Cork warts recorded on the lower surface of the leaf in *Pachyloma* sp. **Epidermis** sometimes consisting of gelatinous cells with wide lumina; papillose on the upper surface in certain species of *Aciotis*, *Allomorpha*, *Bertolonia*, *Clidemia*, *Conostegia*, *Heterotrichum*, *Leandra*, *Marcetia*, *Medinilla*, *Miconia*, *Monochaetum*, *Opisthocentra*, *Rhynchanthera*, *Sonerila*; and on the lower surface of species of *Bellucia*, *Dichaetanthera*, *Dissochaeta*, *Henriettea*, *Kibessia*, *Mecranium*, *Miconia*, *Pternandra*, *Tetrazygia*; locally consisting of 2 or more layers on the upper surface of species of *Comolia* and *Miconia*; wholly or locally palisade-like on the upper side in species of *Calycogonium*, *Clidemia*, *Leandra*, *Miconia*, *Ossaea*, *Tetrazygia*; and on the lower side in species of *Miconia*. **Hypoderm** recorded in species of *Anplectrum*, *Astronia*, *Blakea*, *Calycogonium*, *Charianthus*, *Clidemia*, *Conostegia*, *Dichaetanthera*, *Dissotis*, *Graffenrieda*, *Henriettea*, *Henriettella*, *Kendrickia* (specially thick), *Loreya*, *Macairea* (especially above the vascular bundles of the veins), *Marcetia*, *Marumia*, *Mecranium*, *Medinilla* (occupying half the thickness of the lamina in some species), *Meriania*, *Miconia*, *Microlepis*, *Mouriria*, *Ochthocharis*, *Pachyloma*, *Sonerila*, *Tetrazygia*, *Tibouchina*.

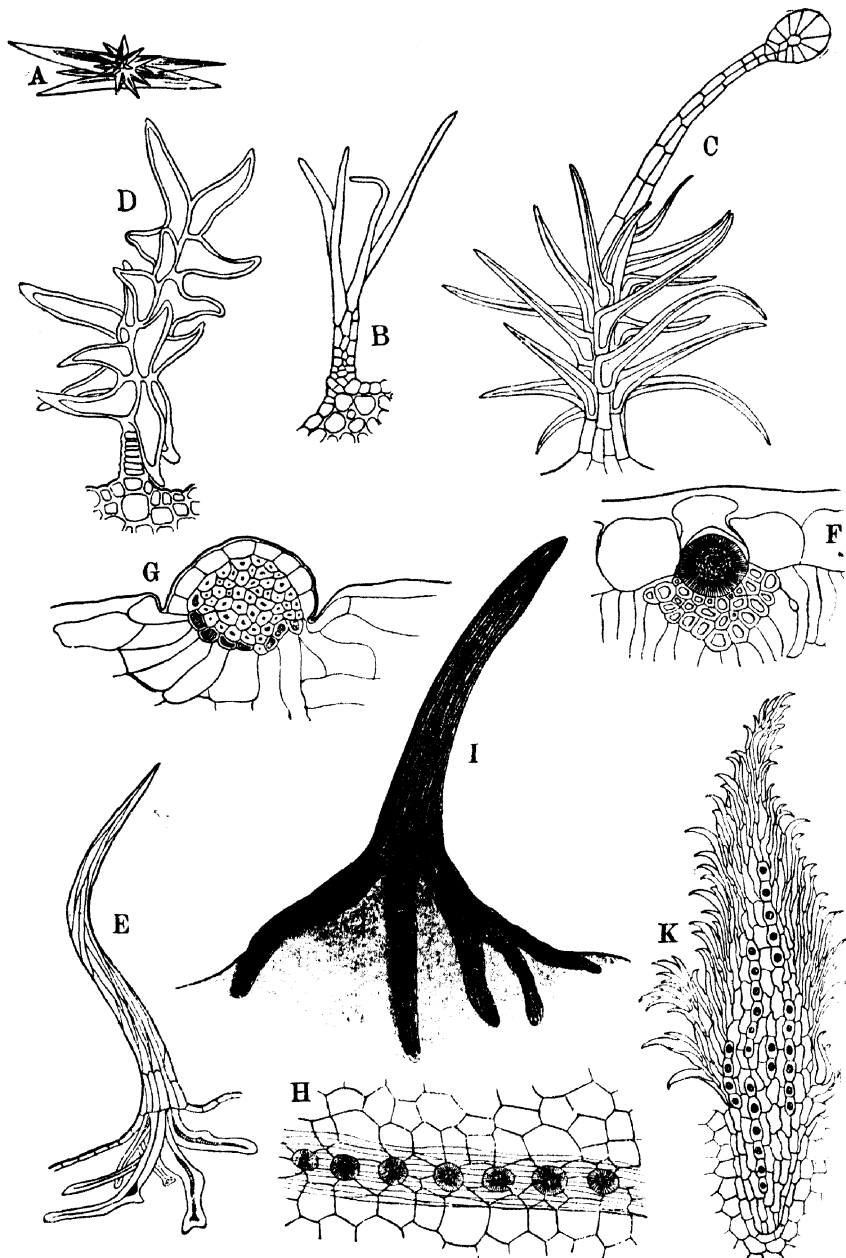


FIG. 144. MELASTOMACEAE

A, Clustered crystal of *Centradenia floribunda* Planch. B, Brush-like shaggy hair from the leaf of *Tococa* sp. C, Shaggy hair of candelabra type with glandular head in *Pyramia*. D, Candelabra hair of *Medinilla* sp. E, Shaggy hair on the leaf of *Tibouchina aemula* Cogn. with root-like base to the hair. F, Section through a bundle of sclerenchyma-fibres (hair-base), running beneath the epidermis of the leaf, as a prolongation of the hair in *Tibouchina chamaecistus* Cogn. G, Section through the base of a shaggy hair, adpressed to the leaf in the same plant. H, Base of a shaggy hair in surface-view in the same species. I, Shaggy hair of *Tibouchina decemcostata* Cogn., sending out several bundles of sclerenchyma-fibres at the base, which run subepidermally. K, Scale-like shaggy hair of *Tibouchina mathaei* Cogn.—A, C, and K after Pflaum, B and D after Lignier; the remainder by Solereder.

Stomata very variable in size, present on both surfaces or confined to the lower side; surrounded by ordinary (often 3) epidermal cells in mature leaves (ranunculaceous to cruciferous); often accompanied by caryophyllaceous types in species of *Bertolonia*, *Marcetia*, *Medinilla*, *Microlicia*, *Oxyspora*, *Sonerila*, and other closely related genera; rubiaceous in *Memecylon*, *Miconia*, and related genera. Stomata sometimes with their pores parallel to one another and to the median vein of the leaf in *Dissotis*, *Microlicia*, *Osbeckia*, *Pterolepis*; confined to variously shaped pits with wide or narrow openings in most species of *Mouriria* (Fig. 138 c); arranged in groups on the inside, and more rarely on the outside, of **ant domatia** in species of *Myrmidone* and *Tococa*, as well as on the lower surface of the leaf in species of *Calycogonium*, *Leandra*, *Ossaea*. **Mesophyll**. Palisade tissue consisting of 2 or 3 layers of interlocking cells in species of *Bellucia*; 1-layered in some of the species of *Medinilla* examined by de Cordemoy (472); including isolated cells with reticulate thickening in species of *Graffenrieda* and *Meriania* and sclerosed cells in species of *Medinilla*. Cells of the spongy mesophyll provided with local thickenings, recalling those of certain Menispermaceae, in species of *Anplectrum*, *Graffenrieda*, *Medinilla*, *Melastoma*, *Meriania*, *Ochthocharis*, *Pachyloma*. Spiral tracheids recorded in the mesophyll of a few species of *Aciotis*, *Bellucia*, *Henriettea*, *Sonerila*, and sclerenchymatous cells of various kinds in species of *Gravesia* (de Cordemoy 471), *Henrietella*, *Huberia*, *Lavoisiera*, *Leandra*, *Macairea*, *Medinilla*, *Memecylon*, *Miconia*, *Microlicia*, *Mouriria*, *Ossaea*, *Plethiandra*; those of *Memecylon* and *Mouriria* stated by Solereder to be of considerable specific diagnostic value. (The more detailed statements on this subject recorded by Solereder need confirmation.) In this connexion, reference must be made to the recent interesting study by Foster (697) of the foliar sclereids in *Mouriria*. Foster observed that the range of form exhibited by these elements in different species of *Mouriria* is quite considerable, and he recognized 4 main types. The sclereids were found to differ from those of many other genera in which they have been studied, in being associated with the terminations of the veins, rather than lying in the mesophyll independently of the vascular system. This raises the question of whether they are homologous with vascular elements. From the taxonomic standpoint, Foster concluded that the sclereids provide a good generic character for *Mouriria*, but feels that their value in the identification of species cannot, at present, be fully assessed. Nevertheless he lists species in which each of his 4 types of sclereid occur, but issues a warning that 'a number of the entities used in the present survey may subsequently prove to have been incorrectly determined'. Vascular bundles of the **veins** more often accompanied by collenchyma than by well-developed sclerenchyma; the latter, when present, sometimes situated below the epidermis and not in direct contact with the vascular bundles in species of *Chaetostoma*, *Lavoisiera*, *Microlepis*, *Microlicia*. Vertically transcurrent veins recorded in *Charianthus*, *Clidemia*, *Henriettea*, *Leandra*, *Miconia*, *Tetrazygia*, *Tococa*. Elongated rod cells said to occur in the parenchymatous ground tissue of the veins in a number of genera.

Petiole (Fig. 143 A-C, G, and I). Transverse sections through the distal end in nearly all of the species examined exhibit an arc of widely spaced vascular bundles, frequently accompanied by subsidiary strands, the latter often being

very numerous and usually situated towards the adaxial side. Vascular structure quite complex in some species. The petiolar vascular structure would be of considerable diagnostic value if better known. Ground tissue of the petiole seen to be supported by scattered stone cells in species of *Medinilla* and *Miconia*.

Crystals usually clustered (Fig. 144 A, F, and H), those in the mesophyll sometimes especially large and appearing as transparent dots in the leaf. Styloids occur, either alone or together with other types of crystal, in *Astronia*, *Beccarianthus*, *Bellucia*, *Calycogonium*, *Centradenia*, *Henriettea*, *Henriettella*, *Kibessia*, *Loreya*, *Memecylon*, *Mouriria*, *Myriaspora*, *Pternandra*.

Developmental anatomy. The developmental anatomy of the leaf of *Heterotrichum macrodon* Planch. and *Clidemia hirta* Don. has been described by Weidt (2385).

AXIS

YOUNG STEM (Fig. 143 D and F)

Frequently winged and provided with vascular bundles in the wings, e.g. in *Centradenia*, *Medinilla*, *Tibouchina*. **Hairs** similar to those on the leaf also occur on the stem. **Cork** arising superficially in *Adelobotrys*, *Astronia*, *Beccarianthus*, *Bertolonia*, *Blakea*, *Blastus*, *Boerlagea*, *Bredia*, *Calvoa*, *Calycogonium*, *Caronia*, *Charianthus*, *Clidemia*, *Conostegia*, *Dalenia*, *Diplarpea*, *Henriettea*, *Henriettella*, *Heterotrichum*, *Kendrickia*, *Loreya*, *Mecranium*, *Medinilla* (pro parte), *Medinillopsis*, *Miconia*, *Microphysa*, *Myriaspora*, *Ossaea*, *Oxyspora*, *Pachyanthus*, *Pachycentria*, *Platycentrum*, *Plethiandra*, *Salpinga*, *Tetrazygia*, *Topobea*; originating in the pericycle in *Amphorocalyx*, *Anerincleistus*, *Benevidesia*, *Calophysa*, *Calyptrilla*, *Centronia*, *Kibessia*, *Meriania*, *Microlicia*, *Mouriria*, *Ochthocharis*, *Octopleura*, *Osbeckia*, *Sagraea*, *Sakersia*, *Tibouchina*; originating in the inner part of the cortex in at least 1 species of *Melastoma* (Fig. 143 D). Cork cells with 1-sided thickenings on the inner tangential walls in *Astronia*, *Dichaetanthera*, *Henriettea*, *Medinilla* (pro parte) (de Cordemoy 472), *Mouriria*. Cork homogeneous in *Dissotis*; consisting of alternating layers of flattened and tall cells respectively in *Barbeyastrum*, *Comolia*, *Heeria*, *Lavoisiera*, *Marcetia*, *Microlicia*, *Osbeckia*, *Pterolepis*, *Tibouchina*. Cork sometimes replaced by **aerenchyma** originating in the pericycle of submerged parts of the stem and older roots of marsh plants included in *Acisanthera* and *Rhynchanthera*. Primary **cortex** containing stone cells, sometimes arranged in groups, in species of *Adelobotrys*, *Axinaea*, *Barthea*, *Blakea*, *Blastus*, *Centronia*, *Graffenrieda*, *Medinilla* (de Cordemoy 472), *Meriania*, *Miconia*, *Myriaspora*, *Ossaea*, *Oxyspora*, *Pachyanthus*, *Pachycentria*, *Pogonanthura*, *Tetrazygia*; stone cells sometimes arranged in a ring in *Conostegia*, *Dissochaeta*, *Mecranium*, *Memecylon*, *Meriania*, *Myriaspora*, *Omphalopus*. Fibres observed in the cortex of a species of *Melastoma*. **Endodermis** usually well defined; in many species composed of thin-walled cells, but stated to include cells with U-shaped thickenings in species of *Anerincleistus*, *Calophysa*, *Dichaetanthera*, *Kibessia*, *Memecylon*, and *Mouriria*; seen to possess casparian thickenings in *Sonerila*; suberized in *Gravesia* and *Medinilla*, according to de Cordemoy (472). **Pericycle** never provided with a composite and continuous ring of sclerenchyma, but contain-

ing a variable proportion of fibres or thickened cells in species of *Blakea*, *Calypptrella*, *Centronia*, *Creochiton*, *Henriettella*, *Kibessia*, *Loreya*, *Memecylon*, *Meriania*, *Plethiandra*, *Topobea*.

Phloem and **xylem**, in the genera represented in the Kew slide collection, in the form of continuous cylinders traversed by narrow rays. Vessels with simple perforations. **Pith** very broad in many genera; consisting of lignified or unlignified cells, sometimes including stone cells or scattered fibrous cells.

Intraxylary phloem (Fig. 143 D and F) universally present in the very considerable number of investigated species, including many not mentioned by name in the text; intraxylary phloem somewhat reduced in *Gravesia* according to de Cordemoy (471). **Interxylary phloem** recorded in *Kibessia*, *Memecylon* (Fig. 143 F) (in the root as well as in the stem), *Mouriria*, *Pternandra*. (See also under 'Included Phloem' on p. 647.) Cortical and/or **medullary bundles**, often with central xylem, but the latter sometimes very much reduced or absent, occur in many but not all genera and species; their number and distribution varying even within a single species. Cortical bundles most frequent in species with rectangular stems; said to represent the lateral strands of the leaf trace, or, more rarely, the midrib itself. The medullary bundles stated to be continuous with the intraxylary phloem. The distribution of medullary and cortical bundles is of some value for the diagnosis of tribes and genera. (See table below and Solereder for further details.)

<i>Medullary bundles alone</i>			<i>Cortical bundles alone</i>
Adelobotrys	*Conostegia	Microphysa	*Axinandra
Allomorpha	Creochiton	Monolena	Cambessedesia
Amphiblemma	Dinophora	Myrridone	Castratella
(pro parte)	Diolena	Nerophila	Chaetostoma
Anaectocalyx	Diplarpea	Ochthocharis	*Lavoisiera
*Anplectrum	Dissochaeta	Omphalopus	*Marcetia
*Astronia	Driessenia	*Ossaea	*Microlicia
*Axinaea	Eriocnema	Oxyspora	Poteranthera
Behuria	Graffenrieda	Pachyanthus	*Pyramia
Bellucia	Gravesia	Pachycentria	*Rhynchanthera
Benevidesia	(de Cordemoy 471)	Phornothamnus	Stenodon
Bertolonia	Heterotrichum	Phyllagathis	Trembleya
*Blakea	Huberia	Platycentrum	Tulasnea
Blastus	Kendrickia	Pleiochiton	
Boerlagea	Leandra	Plethiandra	
Bredia	Lithobium	Pterocladon	
Brittenia	Macrocentrum	Rousseauxia	
Calvoa	*Maieta	Sakersia	
*Calycogonium	Marumea	Salpinga	
Calypptrella	Mecranium	*Tetrazygia	
Carionia	*Medinilla	*Tococa	
Catocoryne	Medinillopsis	*Topobea	
Centronia	*Meriania	Triolena	
Charianthus	*Miconia	Veprecella	
*Clidemia			

* Recorded in 3 or more species. Recorded only in 1 or 2 species in genera not marked with a star.

Medullary and cortical bundles		Medullary and cortical bundles absent
Acanthella	Guyonia	Amphiblemma (pro parte)
Aciotis	*Heeria	Anerincleistus
*Acisanthera	Macairea	Barthea
Amphorocalyx	*Melastoma	Bisglaziovia
Antherotoma	Microlepis	Calvoa
Appendicularia	Monochaetum	*Fritszchia
*Arthrosterma	Nepsera	*Gravesia
Barbeyastrum	Osbeckia	*Henriettea
Brachyotum	Otanthera	*Henriettella
Bucquetia	Pterogastra	*Kibessia
Centradenia	Pterolepis	Loreya
*Chaetolepis	Purpurella	*Memecylon
*Comolia	Rhexia	*Mouriria
Desmoscelis	Rhodosepala	Opisthocentra
Dicellandra	Schwackaea	Phyllagathis
*Dichaetanthera	Svitramia	*Pternandra
Dionychia	*Tibouchina	Sarcopyramis
Dissotis	Tristemma	*Sonerila
Ernestia		

* Recorded in 3 or more species. Recorded in only 1 or 2 species in genera not marked with a star.

Secretory cells, with unidentified, amorphous contents, fairly common in unligified tissues, especially in the cortex and phloem, but varying in frequency in different species. de Cordemoy (468) refers to a system of tanniferous elements in the phloem of certain species of *Dichaetanthera*. **Crystals** almost exclusively clustered in the species represented in the Kew slide collection, solitary types seen only in *Memecylon*; frequently abundant, especially in the cortex or phloem. Cristarque cells (i.e. cells with cellulose thickenings to the inner walls, each cell containing a solitary crystal), recorded by de Cordemoy (470) in the exodermis of certain species belonging to the Osbeckiaceae.

WOOD (Fig. 145)

Vessels mostly small (less than 100 μ mean tangential diameter), very small (50–100 μ) in *Brachyotum*, *Calycogonium*, *Henriettella*, *Leandra*, *Mecranium*, and *Mouriria* p.p., medium-sized (100–200 μ) in some species of *Astronidium*, *Centronia*, *Conostegia*, *Dactylocladus*, *Dissochaeta* (2158), *Henriettea*, *Huberia*, *Meriania*, *Miconia*, and *Pternandra*; usually with numerous small radial multiples and commonly with irregular clusters, though occasionally tending to be mostly solitary in some species of *Memecylon*, e.g. *M. edule* Roxb. and *M. subfurfuraceum* Merr.; multiples of 4 or more cells moderately common in *Graffenrieda*, *Huberia*, *Miconia* p.p., and *Tococa*, clusters most pronounced in *Brachyotum*, *Henriettella*, *Heterotrichium*, *Mecranium*, *Melastoma*, *Miconia* p.p., *Rhynchanthus*, and *Tibouchia*; with a tendency to a tangential pattern in *Memecylon* p.p. and *Rhynchanthera*, and a radial or flame-like pattern in *Mouriria*, e.g. in some specimens of *M. parviflora* Benth. and *M. pseudo-geminata* Pitt.; 4–80, mostly 7–25 per sq. mm., seldom giving the appearance of being crowded even when numerous, less than 5 per sq. mm. in *Conostegia*, *Dactylocladus*, and *Meriania*, 20–40 per sq. mm. in *Aciotis*, *Astronia*, *Bellucia*,

Brachyotum, *Dissotis*, *Henriettella*, *Huberia*, *Medinilla*, and *Memecylon* p.p., more than 40 per sq. mm. in *Calycogonium*, *Clidemia*, *Leandra*, *Mecranium*, *Memecylon* p.p., *Mouriria* p.p., and *Rhynchanthera* p.p. Perforations exclusively simple. Intervascular pitting typically alternate, but scalariform in *Astronia*, *Blastus* (1206), and *Medinilla*, commonly very small to minute, e.g. in *Bellucia*, *Calycogonium*, *Clidemia*, *Henriettea*, *Henriettella*, *Heterotrichum*, *Leandra*, *Mecranium*, *Memecylon*, *Miconia*, *Mouriria*, *Ossaea*, *Pachyanthus*, *Tetrazygia*, and *Tococa*, moderately large in *Dactylocladus*, *Huberia*, *Meriania*, and *Tibouchina*; occasionally with coalescent apertures, e.g. in *Macairea* and *Memecylon*; pits to parenchyma simple and elongated, with their long axes horizontal, oblique, or axial, in *Astronia*, *Astronidium*, *Brachyotum*, *Calycogonium*, *Calyptrilla*, *Centronia*, *Conostegia*, *Dissotis*, *Graffenrieda*, *Henriettea*, *Huberia*, *Loreya*, *Macairea*, *Mecranium*, *Medinilla*, *Melastoma*, *Meriania*, *Pternandra* (pits almost round), *Rhynchanthera*, *Tibouchina*, and *Tococa*; similar to the intervacular pitting in the other genera, which include all those of the Memecyleae. Usually without solid deposits; Williams (2430) refers to calcium deposits in *Miconia* and *Tococa*; tyloses observed or reported in *Astronia*, *Huberia*, *Kibessia*, *Medinilla*, *Pternandra*, *Rhynchanthera*, and *Tococa*, those of *Medinilla* sclerosed. Mean member length 0.3–0.8 mm. **Parenchyma** in most of the genera paratracheal only and varying from a few cells (scanty) to a complete sheath round the vessels (vasicentric); variable and difficult to classify in the other genera, but some paratracheal always present; aliform, with blunt or long uniseriate extensions from the vessels in the Memecyleae, i.e. in *Dactylocladus* (Fig. 145 A), *Memecylon* p.p., and *Mouriria* p.p.; in narrow, apparently apotracheal bands 1–2 cells wide in *Clidemia*, *Mouriria* p.p., and *Tococa*; in broader, regular to wavy bands in *Calyptrilla*, *Graffenrieda*, *Kibessia*, and *Meriania* (Fig. 145 I); in patches or discontinuous bands, suggesting fragments of the broad bands described above and sometimes comparable in distribution to the groups of septate fibres or included phloem described below, in *Conostegia*, *Ossaea*, *Pachyanthus*, and *Tibouchina* (Fig. 145 G), often with conspicuous intercellular spaces; diffuse parenchyma present in *Kibessia*, *Memecylon*, and *Mouriria* (Fig. 145 H) and, according to Janssonius (1154), in 1 species of *Melastoma*; with apparently terminal bands in some species of *Dissotis* and *Mouriria*. Seldom with gummy contents and crystals not observed. Strands mostly of 4–6, occasionally 2 or 8, cells; Janssonius (1154) notes occasional fusiform cells in *Kibessia azurea* DC. **Rays** of the Melastomoideae typically exclusively uniseriate or with only local biseriations, and composed of upright and square cells, with very few or no truly procumbent cells; occasionally with moderately numerous procumbent cells (Kribs's Type Heterogeneous III), e.g. in *Astronidium* and *Pachyanthus*, and sometimes composed almost entirely of procumbent cells, e.g. in *Axinaea* (1886) and *Conostegia*. In *Centronia*, *Macairea*, and *Medinilla* some of the rays are multiseriate (2–4 cells wide), but they are essentially similar to the uniseriate type described above, being composed mainly of square or upright cells and presenting in tangential section a loose mixture of cells of all sizes and shapes (Fig. 145 D); multiseriate rays also present, according to Record and Hess (1886) in *Blakea* and *Topobea*. In the Astronioideae and Memecyleae the rays are up to 2–5 cells wide in *Kibessia*, *Memecylon*, *Mouriria* p.p., and *Pternandra*, and except in *Mouriria*, tend to be of 2 distinct sizes; the

larger rays with a compact central portion of small procumbent cells and 1-3 marginal rows of square or upright cells, the uniseriate rays low and often only 1 cell high; in *Pternandra* the central portion of the larger rays is largely disintegrated in dry specimens, but appears to consist of tissue similar to that

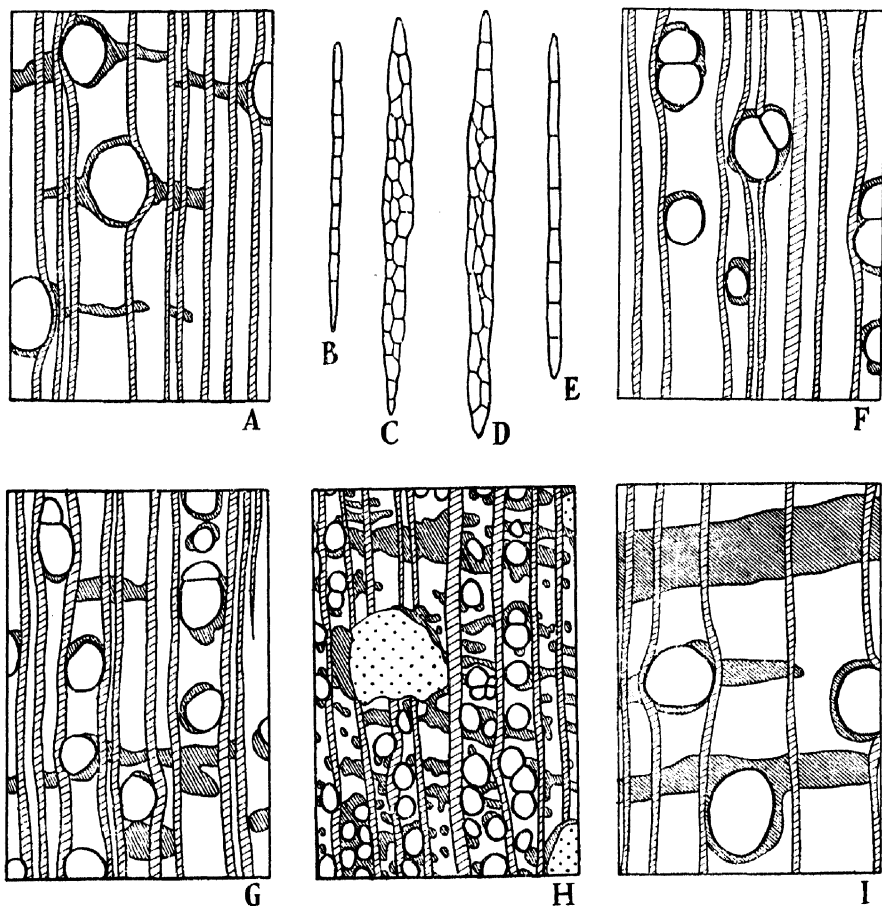


FIG. 145. MELASTOMACEAE

A, *Dactylocladus stenostachys* Oliv. B, *D. stenostachys* Oliv. C, *Mouriria pseudogeminata* Pittier. D, *Centronia excelsa* Triana. E, *Meriania urceolata* Triana. F, *Centronia excelsa* Triana. G, *Tibouchina lepidota* Baill. H, *Mouriria pseudogeminata* Pittier. I, *Meriania urceolata* Triana.

of the axial strands of included phloem; in *Mouriria* the rays, whether multi-seriate or wholly uniseriate, as in *M. parviflora* Benth. and *M. cyphocarpa* Standl., are similar to those described above for the Melastomoideae, as are also the wholly uniseriate rays of *Astronia* and *Astronidium*; in *Dactylocladus* the rays, though uniseriate only, differ from those of the Melastomoideae, except *Axinaea* and *Conostegia*, being composed entirely of procumbent cells apart from an occasional marginal row of square cells. Usually with 7-25 rays per mm.; species with only uniseriate rays mostly with 13-17 per mm., fewer in *Brachyotum* and *Meriania* and more than 17 per mm. in some species of

Aciotis, *Clidemia*, and *Miconia*; species with multiseriate rays mostly with 7-13 per mm., but up to 16 in some species, e.g. of *Memecylon*. Very commonly with gummy contents, which often fill the cells; crystals not observed. **Fibres** with distinctly bordered pits, usually equally numerous on both radial and tangential walls, in most of the genera of the Astronioideae and Memecyleae, i.e. in *Dactylocladus*, *Kibessia*, *Memecylon*, *Mouriria*, and *Pternandra*, and with thick walls except in *Dactylocladus*; with simple pits, thin walls and septa in *Astronia* and *Astronidium*. In the Melastomoideae: pits simple and usually more numerous (often in more than 1 row) on the radial walls; Solereder refers to narrow borders in *Sonerila elegans* Wight; commonly septate in *Bellucia*, *Blastus* (1206), *Calycogonium*, *Henriettea*, *Henriettella*, *Heterotrichium*, *Huberia*, *Leandra*, *Macairea*, *Mecranium*, *Medinilla*, *Melastoma*, *Miconia*, *Ossaea*, *Pachyanthus*, *Tetrazygia*, *Tibouchina*, and *Tococa*; with occasional fine septa in most of the other genera, but septa not observed or very rare in *Brachyotum*, *Calyptralla*, *Graffenrieda*, *Meriania*, *Rhexia* (2158), and *Rhynchanthera*. Thinner-walled patches or bands of fibres, with conspicuous intercellular spaces, very characteristic; the septate fibres sometimes limited to these groups; Janssonius (1154) states that such septate fibres in *Astronia*, *Medinilla*, and *Melastoma* are shorter than the surrounding non-septate fibres. In *Tibouchina* septate fibres occur in similar groups, which, however, consist mainly of parenchyma cells; walls usually moderately thin and often with a mucilaginous layer, thick in *Meriania*; commonly in very distinct radial rows. Mean length 0.5-1.2 mm. **Included (interxylary) phloem** of the 'foraminate' type, with isolated strands of included phloem given off externally by the cambium (2158), present in some genera of the Astronioideae and Memecyleae, i.e. in *Kibessia*, *Lijdenia*, *Memecylon*, *Mouriria* (Fig. 145 H), *Olisbea* (1851), and *Pternandra*.

ANOMALOUS STRUCTURE

See last paragraph and Inter- and Intraxylary Phloem under 'Young Stem'.

ROOT

Tuberous roots, which occur in certain species of *Medinilla*, stated by de Cordemoy (470, 472) to consist mainly of secondary phloem largely composed of parenchyma.

TAXONOMIC NOTES

FROM WOOD STRUCTURE

The woods of the Astronioideae and Memecyleae are distinguishable from those of the Melastomoideae, particularly on account of their fibre-tracheids, included phloem, and multiseriate rays. *Astronia* and *Astronidium*, however, are exceptions, being indistinguishable from the Melastomoideae. F. Markgraf (1442) considers these 2 genera to be separate and, though a direct comparison of the woods has not been possible, from descriptions (376) there appear to be some differences, e.g. in type of perforation.

Included phloem occurs only in the Astronioideae and Memecyleae, but is not always present. The following genera have normal wood: *Astronia*, *Astronidium*, *Axinandra*, *Beccarianthus*, *Dactylocladus*, and *Plethiandra*.

Janssonius (1154) considers that *Kibessia*, *Memecylon*, and *Mouriria* should

be treated as a separate family between the Melastomaceae and the Myrtaceae. *Pternandra* (not investigated by Janssonius) would fall into the same group and possibly also *Dactylocladus*, though this differs in some respects.

ECONOMIC USES

No products of great economic importance are derived from this family, but a number of species are commonly cultivated for ornamental purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Acanthella, *Aciotis*, *Acisanthera*, *Adelobotrys*, *Allomorpha*, *Amphiblemma*, *Amphorocalyx*, *Anaectocalyx*, *Anerincleistus*, *Anplectrum*, *Antherotoma*, *Appendicularia*, *Arthrostema*, *Astronia*, *Axinaea*, *Axinandra*, *Barbeyastrum*, *Beccarianthus*, *Behuria*, *Bellucia*, *Benevidesia*, *Bertolonia*,* *Bisglaziovia*, *Blakea*, *Blastus*, *Boerlagea*, *Brachyotum*, *Bredia*,* *Brittenia*, *Bucquetia*, *Calvoa*, *Calycogonium*, *Calypptrella*, *Cambessedesia*, *Carionia*, *Castratella*, *Catocoryne*, *Centradenia*,* *Centronia*, *Chaetolepis*, *Chaetostoma*, *Charianthus*, *Clidemia*,* *Comolia*, *Conostegia*, *Creochiton*, *Dalenia*, *Desmoscelis*, *Dicellandra*, *Dichaetanthera*, *Dinophora*, *Diolena*, *Dionychia*, *Diplarpea*, *Dissochaeta*, *Dissotis*, *Driessenia*, *Ernestia*, *Fritzschia*, *Graffenrieda*, *Gravesia*, *Guyonia*, *Heeria*, *Henriettea*, *Henriettella*, *Heterotrichum*, *Huberia*, *Kendrickia*, *Kibessia*, *Lasiandra*, *Lavoisiera*, *Leandra*, *Lithobium*, *Loreya*, *Macairea*, *Macrocentrum*, *Maieta*, *Mecranium*, *Medinilla*,* *Medinillopsis*, *Melastoma*,* *Memecylon*,* *Meriania*, *Miconia*,* *Microlepis*, *Microlicia*, *Microphysa*, *Monochaetum*, *Monolena*, *Mouriria*, *Myrmidone*, *Nepsera*, *Ochthocharis*, *Omphalopus*, *Opisthocentra*, *Osbeckia*, *Ossaea*, *Otanthera*, *Oxymeris*, *Oxyspora*, *Pachyanthus*, *Pachycentria*, *Pachyloma*, *Phornothamnus*, *Phyllagathis*, *Platycentrum*, *Pleiochiton*, *Plethiandra*, *Pogonanthera*, *Poteranthera*, *Pternandra*, *Pterocladon*, *Pterogastra*, *Pterolepis*, *Purpurella*, *Pyramia*, *Rhexia*, *Rhodosepala*, *Rhynchanthera*, *Rousseauxia*, *Sagraea*, *Sakersia*, *Salpinga*, *Sarcopyramis*, *Schwackaea*, *Siphanthera*, *Sonerila*,* *Stenodon*, *Svitramia*, *Tetrazygia*, *Tibouchina*,* *Tococa*, *Topobea*, *Trembleya*, *Triolena*, *Tristemma*, *Tulasnea*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

Melastomatoideae: *Aciotis*, (*Axinaea*), *Bellucia*, (*Blakea*), (*Blastus*), *Brachyotum*, *Calycogonium*, *Calypptrella*, *Centronia*, *Clidemia*, *Conostegia*, (*Dissochaeta*), *Dissotis*, *Graffenrieda*, *Henriettea*, *Henriettella*, *Heterotrichum*, *Huberia*, *Leandra*, *Macairea*, *Mecranium*, *Medinilla*, *Melastoma*, *Menendezia*, *Meriania*, *Miconia*, *Ossaea*, *Pachyanthus*, (*Rhexia*), *Rhynchanthera*, (*Sonerila*), *Tetrazygia*, *Tibouchina*, *Tococa*, (*Topobea*). *Astro-nioideae*: (*Astronia*), *Astronidium*, *Kibessia*, *Pternandra*. *Memecyloideae*: *Dactylocladus*, (*Lijndenia*), *Memecylon*, *Mouriria*, (*Olisbea*).

LITERATURE

(i) *On General Anatomy*

de Cordemoy 468, 470, 471, 472, Foster 697, Ross 1959, Weidt 2385.

(ii) *On Wood Structure*

Bailey 78, Benoist 170, den Berger 182, Burgerstein 310, Chennery 2515, Chalk and Chattaway 362, 376, Cooper and Record 461, Howard 1088, Janssonius 1154, Kanehira 1206, 1209, Kribs 1283, Markgraf 1442, Pfeiffer, H. 1712, Pfeiffer, J. Ph. 1713, Record 1843, 1851, Record and Hess 1886, Record and Mell 1894, Williams 2430.

139. LYTHRACEAE

(FIG. 146 on p. 650; FIG. 147 on p. 652; FIG. 148 on p. 658)

SUMMARY

(i) GENERAL

The most important feature common to the trees, shrubs, and herbs belonging to this widely distributed family is the occurrence of **intraxylary phloem**. Where the vascular system is in the form of bundles, e.g. in the leaf, these are bicollateral. The **hairs** are mostly unicellular or bicellular, although more complex types also occur. **Mucilaginous cells** are fairly common in the leaf epidermis; and occasionally elsewhere in the lamina. The somewhat variable **stomata** are ranunculaceous in most species. **Secretory cavities** are absent except from 1 species of *Cuphea* and in *Heteropyxis*, but the last genus ought probably to be excluded from the Lythraceae. The **cork** in the stem, which generally arises in the inner part of the pericycle, is often somewhat loosely constructed, and may be replaced or accompanied by aerenchyma. **Interxylary phloem** recorded in the root of *Lythrum salicaria* Linn.

(ii) WOOD

Vessels small to medium-sized, ring-porous in some species, perforations simple, intervacular pitting alternate, small to medium-sized, vested, pits to parenchyma similar or large and simple; members of medium length to moderately short. **Parenchyma** predominantly paratracheal, scanty or vasicentric to aliform and confluent, sometimes with numerous septate crystalliferous cells. **Rays** exclusively uniseriate or up to 2-3 cells wide, heterogeneous to homogeneous. **Fibres** with simple pits and commonly septate, thin-walled fibres containing starch or crystals sometimes occurring with a parenchyma-like distribution; of medium length to moderately short.

LEAF

Usually dorsiventral, e.g. in *Adenaria*, *Ammannia*, *Crenea*, *Cuphea*, *Ginora*, *Lafoenisia*, *Lagerstroemia*, *Lawsonia*, *Nesaea*, *Physocalymma*, *Woodfordia*; isobilateral in *Pemphis acidula* Forst.; homogeneous in *Peplis* according to Gin (785). **Hairs** (Fig. 146) include the following types, the first being the most widely distributed. (i) Unicellular or bicellular, elongated in some but short and resembling papillae in other species of *Adenaria*, *Cuphea*, *Decodon*, *Diplusodon*, *Ginora*, *Grislea*, *Lagerstroemia*, *Lythrum*, *Nesaea*, *Pemphis*, *Peplis*, *Physocalymma*, *Pleurophora*, *Woodfordia*. (ii) Simple, unicellular, placed obliquely or almost parallel to the surface, e.g. in *Pemphis*, tending to be 2-armed and provided with thickened silicified walls with warts in *Cuphea* (Fig. 146 c). (iii) Tufted or branched and provided with uniseriate

stalks in *Decodon* and *Lagerstroemia*. (iv) Glandular and non-glandular shaggy types in *Cuphea* (Fig. 146 A-B). (v) Spherical glandular hairs, provided with very short stalks, situated in pits and appearing as black dots on the lower side of the leaf, in species of *Adenaria*, *Grislea*, *Lagerstroemia*, *Pemphis*, *Woodfordia* (Fig. 146 D).

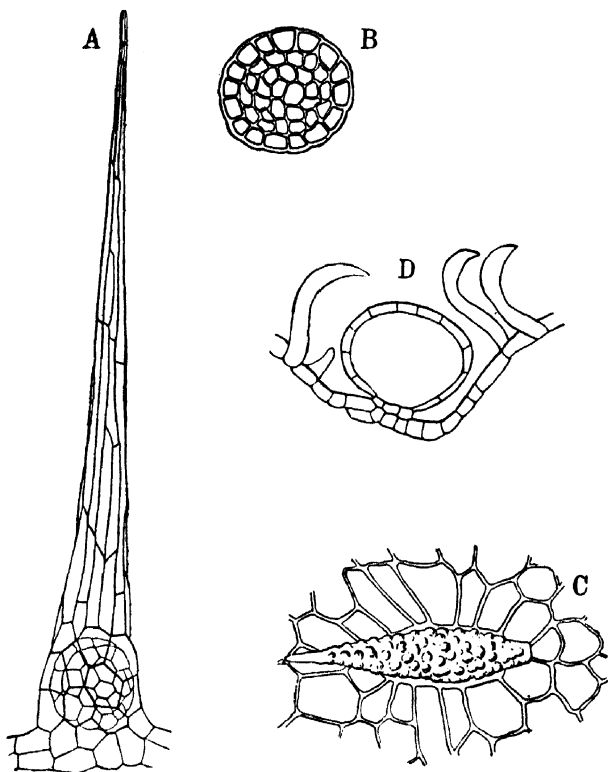


FIG. 146. LYTHRACEAE

A, B, Shaggy hair of *Cuphea lanceolata* Dryand. in Ait. Hort. Kew., with glandular base; the latter cut transversely in B. C, Trichome of *Cuphea appendiculata* Benth. D, Section of an external gland of *Woodfordia floribunda* Salisb.—A, B, after Martinet, C, D, by Solereder.

Epidermis containing mucilaginous cells in species of *Adenaria*, *Ammannia*, *Cuphea*, *Diplusodon*, *Ginora*, *Lafoensia*, *Lagerstroemia*, *Lawsonia*, *Lythrum*, *Nesaea*, *Pemphis*, *Peplis*, *Woodfordia*, and probably other genera as well. Mucilaginous cells also occur in other parts of the lamina of *Diplusodon*, *Lagerstroemia*, *Nesaea*, *Pemphis*, &c. Cells of the upper epidermis sometimes horizontally divided in *Ginora*, *Lagerstroemia*, *Pemphis*; occasionally papillose. **Hypoderm** recorded in *Ginora* and *Lagerstroemia*. **Stomata** confined to the lower surface or present on both sides, usually ranunculaceous; pores approximately parallel to the main vein in species of *Diplusodon*, *Heimia*, *Lythrum*, *Nesaea*, *Pleurophora*. **Mesophyll** of species with dorsiventral leaves containing 1-3 layers of palisade cells.

Vascular bundles of the **veins** bicollateral. Smaller veins vertically trans-

current in species of *Decodon*, *Grislea*, *Lagerstroemia*, *Physocalymma*; those of *Pemphis acidula* Forst. said by Kienholz (1236) to be devoid of sclerenchyma and embedded in aqueous tissue. Storage and terminal tracheids occur in the form of large pitted cells in species of *Crenea*, *Diplusodon*, *Lawsonia*. **Petiole** (Fig. 148 D). Transverse sections through the distal end of the few species represented in the Kew slide collection exhibit a solitary, slightly curved, crescent-shaped, bicollateral, vascular strand, sometimes accompanied by small, circular, accessory bundles in the wings. **Secretory receptacles**, appearing as transparent dots, recorded by Solereder in *Cuphea anagalloidea* St. Hill. and in *Heteropyxis*. (The taxonomic position of *Heteropyxis* is uncertain and it has been variously included in the Lythraceae, Myrtaceae, and in a special family the Heteropyxidaceae.) **Mucilage cells**, see 'Epidermis'. **Crystals** mostly clustered; abundant solitary crystals recorded in association with the veins in *Lagerstroemia*. Small crystalline rods, needles, or granules recorded in *Adenaria*, *Decodon*, *Diplusodon*, *Heimia*, *Lafoensia*, *Lawsonia*, *Lythrum*, *Nesaea*, *Physocalymma*, *Pleurophora*, *Woodfordia*. Small clustered crystals situated in groups of special mesophyll cells occur in *Pemphis*. Clustered or large solitary crystals stated to occur in idioblasts and sometimes to appear as transparent dots in species of *Diplusodon*, *Galpinia*, *Lafoensia*, *Lagerstroemia*, *Nesaea*. Sphaerocrystalline masses of unknown chemical nature recorded in certain species of *Decodon*, *Diplusodon*, *Heimia*, *Lagerstroemia*, *Lythrum*. Anatomical differences in the anatomy of *Cuphea balsamona* Cham. et Schl. collected at different altitudes have been described by Privault (1759). Bodmer (212), in the course of a very detailed investigation of the developmental anatomy of *Lythrum salicaria* Linn., found that submerged leaves are much thinner than those on the aerial part of the stem, but the stomatal frequency was similar in both types of leaf.

AXIS

STEM (Fig. 148 A)

Young stem commonly with 4 or 5 prominent angles, the latter sometimes enlarged to form wing-like expansions. **Cork** generally arising in the inner part of the pericycle in species of *Ammannia*, *Crenea*, *Cuphea*, *Diplusodon*, *Ginora*, *Heimia*, *Lagerstroemia*, *Lawsonia*, *Lythrum*, *Nesaea*; originating in the primary cortex in species of *Lafoensia* (Fig. 148 A) and *Pemphis*. Cork cells very small in species of *Ammannia*, *Crenea*, *Lawsonia*, *Lythrum*, *Nesaea*, *Peplis*. Cork many-layered in species of *Pemphis* and *Pleurophora*; partly composed of phelloid cells in a number of genera; sometimes replaced or accompanied by aerenchyma in *Crenea*, *Cuphea*, *Decodon* (forming a white spongy tissue on the aerial stems of *D. verticillatus* Ell. according to Gin (785)), *Heimia*, *Lythrum*, *Nesaea*, *Peplis*. Primary **cortex** described by Gin (785) as containing a system of intercellular spaces in species of *Ammannia*, *Cuphea*, *Heimia*, *Lythrum*, and 4 large air canals in *Crenea repens* G. F. W. and various species of *Peplis* including *P. portula* Linn. **Endodermis** with casparian thickenings recorded by the same author in species of *Adenaria*, *Cuphea*, *Lagerstroemia*, and *Peplis portula*; composed of cells with uniformly thickened cellulose walls in other species of *Lagerstroemia*; cells thickened on the internal and lateral walls in other species of *Lagerstroemia*, in *Nesaea salicifolia* H. B. et K. and *Physocalymma scaberrimum* Pohl. Sclerenchyma poorly developed

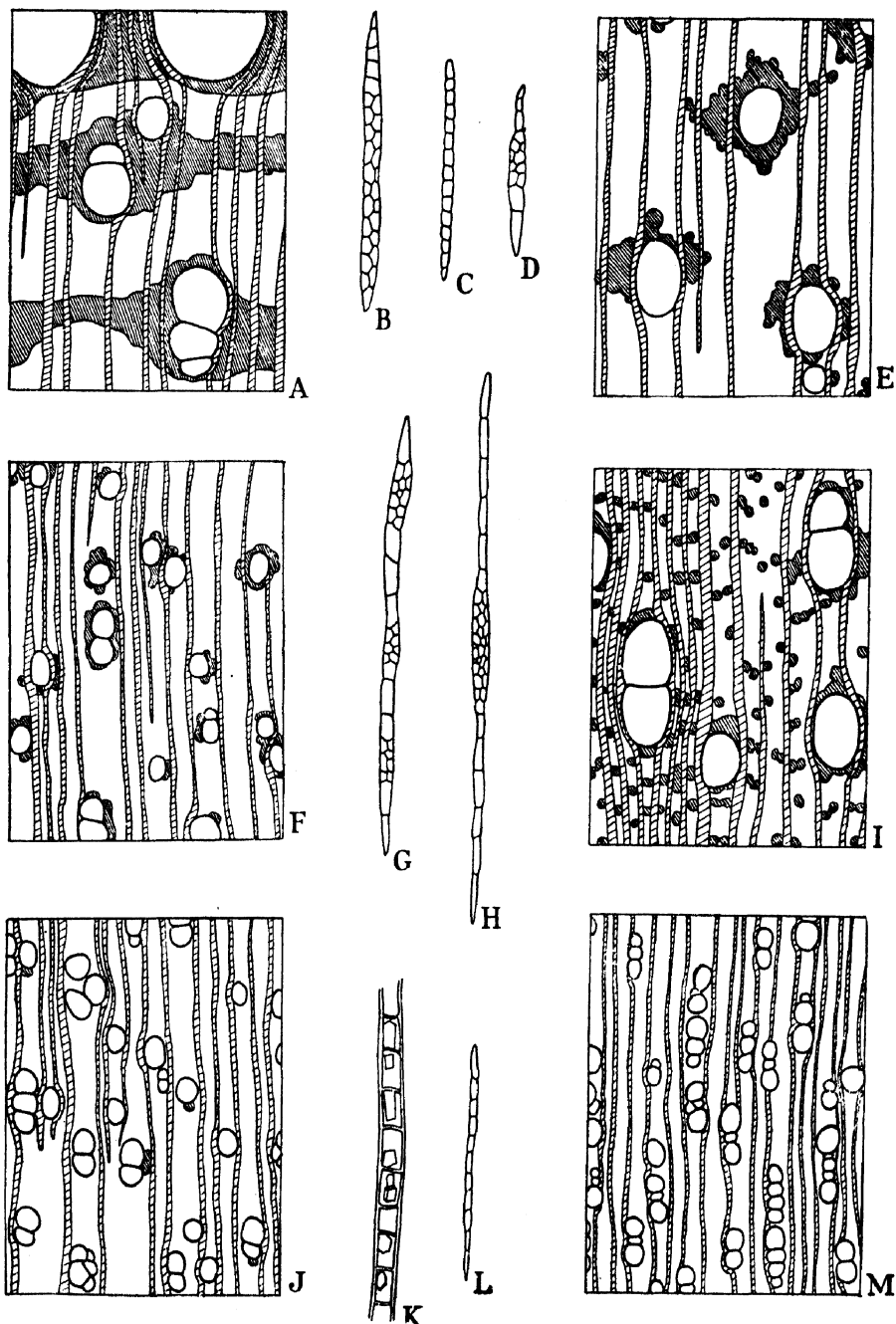


FIG. 147. LYTHRACEAE, A-F; OLINIACEAE, G and J; CRYPTERONIACEAE, H-I; PUNICACEAE, K-M

A, *Lagerstroemia flos-reginae* Retz. B, *L. flos-reginae* Retz. C, *L. ovalifolia* Teysm. D, *Pemphis acidula* Forst. E, *Lafoensia* sp. F, *Pemphis acidula* Forst. G, *Olinia usambarensis* Gilg. H, *Crypteronia paniculata* Blume. I, *C. paniculata* Blume. J, *Olinia cymosa* Thunb. K, *Punica granatum* Linn. Crystalliferous fibre ($\times 200$). L, *P. granatum* Linn. M, *P. granatum* Linn.

in or absent from the **pericycle**, but isolated strands of fibres recorded in *Cuphea*, *Lafoensia*, *Lagerstroemia*, *Lythrum*, or occasionally a sclerenchymatous ring in *Ammannia*, *Diplusodon*, *Lafoensia*, *Lagerstroemia*. **Phloem** sometimes including concentrically arranged crystal cells. Secondary phloem containing fibres in *Lafoensia* and *Lagerstroemia*. Sclerosed cells also noted in the secondary phloem in a few species of *Cuphea* and *Lafoensia* by Gin (785). **Phloem** and **xylem** in the form of continuous cylinders traversed by narrow rays in all of the species represented in the Kew slide collection. Vessels with simple perforations. Xylem of *Cuphea annulata* Koehne said by Gin (785) to appear, in transverse sections, as 2 equal arcs separated by unligified parenchyma.

Intraxylary phloem recorded or observed in *Adenaria*, *Ammannia*, *Crenea*, *Cuphea*, *Decodon*, *Diplusodon*, *Ginora*, *Heimia*, *Lafoensia* (none clearly visible in the specimen illustrated in Fig. 148 A), *Lagerstroemia*, *Lawsonia*, *Lythrum*, *Nesaea*, *Pemphis*, *Peplis*, *Physocalymma*, *Pleurophora*, *Rotala*, *Woodfordia*, and probably occurring throughout the family. **Pith** described by Solereder as strongly sclerosed in *Diplusodon* and *Lagerstroemia*; including large, sclerosed cells in *Adenaria* sp. and *Pemphis acidula* Forst. **Crystals** mostly clustered and frequently abundant, especially in the pith and cortex; solitary types observed in *Lagerstroemia* (see also under 'Phloem' above). **Secretory cells** with unidentified, amorphous contents, present in the unligified tissues of most of the genera examined at Kew.

WOOD (Fig. 147 A-F)

Vessels small (less than 100 μ mean tangential diameter) to medium-sized (100–200 μ); solitary and in multiples of 2 or 3 cells; varying from about 5 per sq. mm. in some species of *Lagerstroemia* to about 20 per sq. mm. in *Pemphis*; ring-porous in most species of *Lagerstroemia*. Perforations simple. Intervascular pitting alternate, small to moderately large; vested (78); pits to ray or wood parenchyma usually similar to the intervascular pitting, but occasionally larger or simple, e.g. in *Lagerstroemia*. Sometimes with deposits of gum and with tyloses in *Lagerstroemia* and *Pemphis*; Pearson and Brown (1679) note 2 types of tyloses in *Lagerstroemia*: (a) thin-walled, large, and cyst-like, and (b) small, sclerenchymatous, copiously pitted, and filled with gum. Mean member length 0.25–0.5 mm. **Parenchyma** predominantly paratracheal; abundant and aliform to confluent in *Lagerstroemia* (Fig. 147 A), tending to be in broad bands in the outer part of the ring; scanty to vasicentric and diffuse in *Pemphis*; scanty paratracheal in most of the American genera (1886), but reported to be abundant in *Adenaria floribunda* H. B. et K. (2430). With conspicuous chambered crystals in *Lagerstroemia*, particularly in cells touching the fibres, the parenchyma cells of normal height but subdivided by septa. Strands commonly of 4 cells. **Rays** exclusively uniseriate in most species of *Lagerstroemia* (2–3 cells wide in most samples of *L. floribunda* Retz.) and in *Lafoensia*, 2 cells wide in *Pemphis*, '1 or 2, rarely 3 cells wide' in the American genera (1886); rays rather low and with many very low uniseriates only 1 or 2 cells high in all the material studied; about 7–17 rays per mm.; homogeneous (Kribs's Type III) in *Lagerstroemia* and, according to Record and Hess (1886), in *Physocalymma*; heterogeneous (Kribs's Types II B and III) in the other genera. Commonly containing gummy deposits,

crystals not observed. References occur in the literature (1801, 2430) to the occurrence of oil or mucilage cells in *Physocalymma scaberrimum* Pohl. but have since been shown to be incorrect (1830, 2430). **Fibres** with simple pits, often septate, e.g. in *Lafoensia* and *Lagerstroemia*; walls usually rather thin, but moderately thick in some species of *Lagerstroemia*, very thick and non-septate in *Pemphis*. Record and Hess (1886) refer to thin-walled fibres with large lumina in numerous distinct parenchyma-like bands in *Ginora* and *Physocalymma*, the cells containing starch at first, but later crystalliferous, and to similar starch-bearing, non-crystalliferous, indistinctly vasicentric fibres in *Lafoensia*. Pearson and Brown (1679) record the occurrence in *Lagerstroemia* of crystals in small locules separated by septa, particularly in fibres contiguous with the rays. Mean length 0.8–1.3 mm.

ROOT

Islands of **interxylary phloem**, formed by secondary differentiation of the xylem parenchyma, recorded by Gin (785) in the root wood of *Lythrum salicaria* Linn.

TAXONOMIC NOTES

Sprague and Metcalfe (2175) concluded, partly on anatomical grounds, that *Rhynchocalyx* should be regarded as a member of the Lythraceae.

ECONOMIC USES

Henna, which is used as a hair dye, consists of the powdered leaves of *Lawsonia alba* Lam., sometimes mixed with other substances. The glabrous, oval, somewhat acuminate leaves are 3–4 cm. long and 1.5–2.5 cm. broad. The tabular epidermal cells are rectilinear or tend to be polygonal in surface view. Some cells of the epidermis are larger than the remainder and mucilaginous. Stomata numerous on both surfaces, surrounded by 3 or 4 ordinary epidermal cells. Mesophyll dorsiventral, with 2 or more layers of palisade tissue towards the upper surface, but locally isobilateral owing to a tendency for the outer cells of the spongy mesophyll to develop as a second palisade. A very detailed description of the history and uses of Henna is included in Gin's (785) thesis. The same author also gives particulars of other members of the family to which medicinal properties have been attributed.

The only genus producing timber of any importance is *Lagerstroemia*. Of this there are several species in the East that produce very similar timbers, which are suitable for high-class joinery work. The best known are those furnishing the timber known as Pyinma, *Lagerstroemia speciosa* Pers. from India and Burma and *L. hypoleuca* Kurz from the Andaman Islands.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Adenaria, Ammannia, Crenea, Cuphea,* Decodon, Diplusodon, Galpinia, Ginora, Grislea, Heimia, Lafoensia,* Lagerstroemia,* Lawsonia, Lythrum,* Nesaea,* Pemphis, Peplis, Physocalymma, Pleurophora, Woodfordia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Adenaria), (Ginora), (Grislea), Lafoensia, Lagerstroemia, Pemphis, (Physocalymma).

LITERATURE

(i) *On General Anatomy*

Bodmer 212, Gin 785, Kienholz 1236, Lourteig 1394, Privault 1759, Sprague and Metcalfe 2175.

(ii) *On Wood Structure*

Bailey 78, Beekman 167, den Berger 179, Besson 186, Collardet 447, Coster 481, Desch 574, Foxworthy 705, Gin 785, Howard 1088, Janssonius 1154, Jones 1191, Kanehira 1206, 1209, 1213, Lecomte 1334, Méniard 1492, Pearson and Brown 1679, Record 1781, 1787, 1801, 1830, 1843, 1851, Record and Hess 1886, Williams 2430.

140. CRYPTERONIACEAE

(FIG. 147 on p. 652)

SUMMARY

(i) GENERAL

A small family consisting of a few species of trees from India and the Malay Archipelago, comprising the single genus *Crypteronia*. The general anatomy has not received much recent attention, but one of the most significant features is the occurrence of **intraxylary phloem**.

(ii) WOOD

Vessels medium-sized, perforations simple, intervacular pitting alternate and small, vestured, pits to parenchyma similar, members of medium length. **Parenchyma** predominantly apotracheal, scattered and in uniseriate lines, also about the vessels. **Rays** up to 2-4 cells wide, markedly heterogeneous with about 10 marginal rows, with conspicuous, canal-like intercellular spaces. **Fibres** with bordered pits, of medium length.

LEAF

Solereider records the occurrence of a single, somewhat collenchymatous layer of **hypoderm**, and the presence of cluster **crystals**.

AXIS

STEM

The following features have been recorded by Solereider. Young stems provided with **wings**, the latter consisting of epidermis and cortical tissue. Secondary **phloem** containing elongated sclerenchymatous elements with numerous pits. **Xylem** in the form of a continuous cylinder traversed by narrow rays. Vessels with simple perforations. **Pith** including scattered prosenchymatous elements, sometimes arranged in groups. **Intraxylary phloem** present.

WOOD (Fig. 147 H-I)

Vessels medium-sized (100-200 μ mean tangential diameter); solitary and in multiples of 2 or 3 cells; 5-8 per sq. mm. Perforations simple. Intervacular pitting alternate, small, pits to ray and wood parenchyma similar to the intervacular pitting; vestured (78). Mean length 0.35-0.7 mm. **Parenchyma** predominantly apotracheal, as scattered cells tending to form irregular uniseriate lines and to be rather more abundant round the vessels.

Strands of 8 or more cells. **Rays** up to 2-4 cells wide; less than 1 mm. high; uniseriates numerous and composed entirely of upright cells; about 20 rays per mm.; markedly heterogeneous (Kribs's Type II A), with up to about 10 marginal rows of square to upright cells. Cells often filled with dark gummy contents. **Fibres** with few and small, but distinctly bordered, pits, mostly on the radial walls. Walls of medium thickness. Mean length about 1.4 mm. **Intercellular canals.** The ray cells are often rounded, with marked radial intercellular spaces between the procumbent cells. Webber (2377) has pointed out that there is no clear-cut distinction between such cavities and intercellular canals, and the family is sometimes listed (1851) among those having radial canals.

TAXONOMIC NOTES

The presence of intraxylary phloem is interesting, since this feature occurs also in the Lythraceae, in which family *Crypteronia* was included in the Bentham and Hooker system.

ECONOMIC USES

One species, *Crypteronia paniculata* Bl. from Burma, is stated by Pearson and Brown (1679) to be used for building and is referred to by Desch (574) as a local substitute for Meranti.

GENUS DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Crypteronia.

LITERATURE

On Wood Structure

Bailey 78, Desch 574, Janssonius 1154, Lecomte 1334, Pearson and Brown 1679, Record 1843, 1851, Webber 2377.

141. OLINIACEAE

(FIG. 147 on p. 652)

SUMMARY

(i) GENERAL

A small family consisting of a few species of shrubs or small trees comprised in the single genus *Olinia* which occurs in St. Helena and South and East Africa. The general anatomy has not received much attention in recent years, but the presence of **intraxylary phloem** is a noteworthy character.

(ii) WOOD

Vessels small, in numerous small multiples, perforations simple, intervascular pitting alternate, very small, vested, pits to ray cells similar, members of medium length. **Parenchyma** very sparse, scanty paratracheal. **Rays** 2 cells wide, markedly heterogeneous with 10 or more marginal rows. **Fibres** with simple pits, septate, of medium length.

AXIS

STEM

The following features have been recorded by Solereder. **Cork** arising in

the sub-epidermis. **Cortex** containing slightly branched sclerenchymatous idioblasts resembling short fibres. Secondary **phloem** including chambered fibres containing solitary crystals. **Xylem** in the form of a continuous cylinder traversed by narrow rays. Vessels with simple perforations. **Intra-xylary phloem** present.

WOOD (Fig. 147 G and J)

Vessels moderately small (50–100 μ mean tangential diameter); solitary and in numerous radial multiples of 2 or 3 cells; with a slight tendency to arrangement in loose oblique rows; about 25 per sq. mm. Perforations simple. Intervascular pitting very small to minute; vestured (78); pits to ray cells similar. Mean member length about 0.5 mm. **Parenchyma** very sparse, limited to an occasional cell touching a vessel; occasionally irregularly banded at the ring boundary (2075). Solereder states that the wood of *Olinia* is noteworthy on account of 'unlignified groups of parenchymatous cells containing solitary crystals and arranged concentrically'; such cells have not been observed by the author. **Rays** up to 2 cells wide, the multiseriate parts short and often more than 1 per ray; less than 1 mm. high; wholly uniseriate rays relatively few; 15–20 rays per mm.; markedly heterogeneous with up to 10, and occasionally more, marginal rows of square to upright cells (Kribs's Type II A). **Fibres** with simple pits, rather more numerous on the radial walls. Septate, but septa not common in *Olinia usambarensis* Gilg. Walls of medium thickness to moderately thick. Mean length about 0.9–1.0 mm.

TAXONOMIC NOTES

The presence of intraxylary phloem is noteworthy, since this feature also occurs in the Lythraceae in which family *Olinia* was included in the Benthams and Hooker system.

ECONOMIC USES

Olinia cymosa Thunb. produces a timber, known as Hard Pear, which is used in South Africa for a variety of purposes (2075).

GENUS DESCRIBED

FOR WOOD STRUCTURE AND GENERAL ANATOMY

Olinia.

LITERATURE

On Wood Structure

Bailey 78, Record 1843, 1851, Scott 2075.

142. PUNICACEAE

(FIG. 147 on p. 652; FIG. 148 on p. 658)

SUMMARY

(i) GENERAL

A small tropical and sub-tropical family of woody, sometimes spiny, shrubs or small trees comprised in the single genus *Punica*. The widely cultivated Pomegranate (*P. granatum* Linn.) is the only species which appears to have

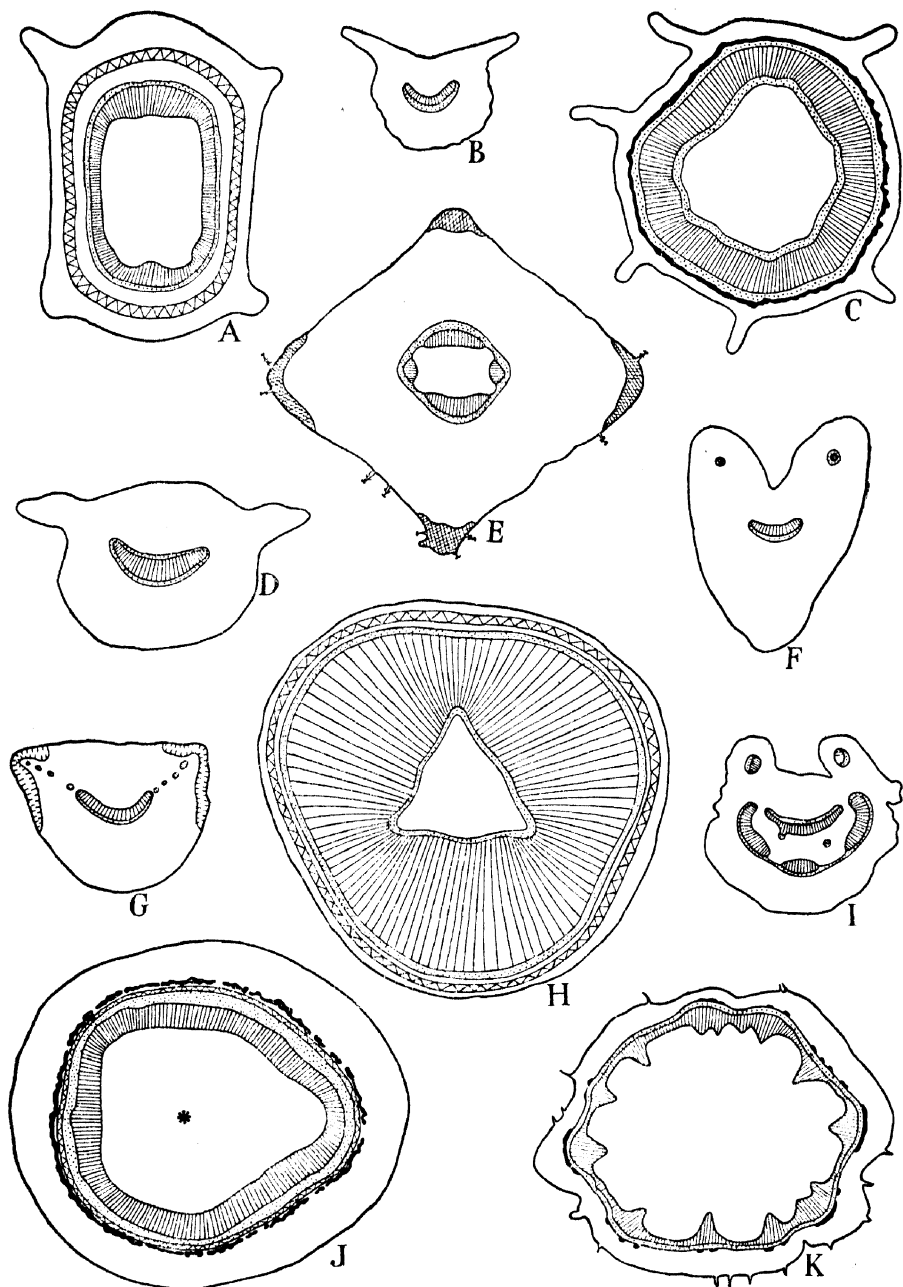


FIG. 148. LYTHRACEAE, A and D; PUNICACEAE, B-C; ONAGRACEAE, G-H and J; LOASACEAE, E-F, I, and K

A, *Lafoensia vandelliana* Cham. et Schlecht. Young stem $\times 33$. B, *Punica granatum* Linn. Petiole $\times 18$. [Adaxial phloem not shown.] C, *P. granatum* Linn. Young stem $\times 18$. [Stems of this species frequently have only 4 wings.] D, *Lagerstroemia indica* Linn. Petiole $\times 18$. E, *Blumenbachia hieronymi* Urb. Stem $\times 8$. F, *B. hieronymi* Urb. Petiole $\times 13$. G, *Oenothera missouriense* Sims. Petiole $\times 8$. H, *Fuchsia magellanica* Lam. Stem $\times 13$. I, *Loasa vulcanica* André. Petiole $\times 13$. J, *Oenothera missouriense* Sims. Stem $\times 13$. K, *Loasa vulcanica* André. Stem $\times 8$.

* Intraxylary phloem omitted.

been investigated anatomically. One of the most interesting features is the occurrence of **intraxylary phloem**.

(ii) WOOD

Vessels very to moderately small, with some multiples of 6–8 cells, perforations simple, intervascular pitting alternate and very small, vested, pits to ray cells similar, members very short. **Parenchyma** absent. **Rays** uniseriate, composed entirely of square and upright cells, very numerous. **Fibres** with simple pits, septate, crystalliferous, very short.

LEAF

Dorsiventral. Cells of the upper **epidermis** with slightly and those of the lower epidermis with very sinuous anticlinal walls. **Stomata** confined to the lower surface; mostly ranunculaceous. **Mesophyll** including 1 layer of palisade cells. Idioblasts, containing very large solitary crystals, present along the boundary between the palisade and spongy tissues. Vascular bundles of the smaller **veins** embedded in the mesophyll, and each surrounded by a sheath of rather large, parenchymatous cells. **Midrib** with an open, crescent-shaped, bicollateral, vascular bundle. Transverse sections through the distal end of the **petiole** (Fig. 148 B) exhibit a similar structure. Solitary and cluster **crystals** present in the lamina and petiole (see also crystal-idioblasts under 'Mesophyll' above).

AXIS

YOUNG STEM (Fig. 148 C)

Provided with wings. **Cork** arising in the inner part of the pericycle. **Pericycle** including a somewhat interrupted ring of fibres along the outer periphery. **Phloem**, in 2- or 3-year-old stems, tending to be separated into strands by the enlarged, triangular, distal ends of the medullary rays. **Xylem** forming a closed cylinder, traversed by narrow rays. Vessels with simple perforations. **Intraxylary phloem** present (Fig. 148 C). **Pith** heterogeneous. Cluster **crystals** abundant in the phloem, those in the secondary phloem tending to be in concentrically arranged sacs. **Secretory cells** with unidentified, amorphous contents, observed in the cortex and pith.

WOOD (Fig. 147 K–M)

Vessels very to moderately small (mean tangential diameter about $50\ \mu$); mostly solitary and in multiples of 2 or 3 cells, but with some multiples of 7 or 8 cells or groups of 3 or 4 cells each almost contiguous radially; about 30 per sq. mm. Perforations simple. Intersvascular pitting alternate and very small, vested (78); pits to ray cells similar. Mean member length about 0.23 mm. **Parenchyma** absent. **Rays** uniseriate, less than 1 mm. high, composed entirely of square and upright cells, about 23 per mm. **Fibres** with simple pits; septate, the septa commonly very numerous and dividing the fibre into a number of chambers each containing 1, or occasionally 2, crystals (Fig. 147 K); the crystalliferous fibres thinner walled and in groups that, in transverse sections, resemble irregular parenchyma bands. Mean length about 0.65 mm.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

Punica was included in the Lythraceae in the Bentham and Hooker system. Its affinity with that family is confirmed by the similarity of the anatomical characters, especially the occurrence of intraxylary phloem.

ECONOMIC USES

Pomegranates are the fruits of *Punica granatum* Linn. The anatomical structure of the dried rind of the fruit, which is used in medicine, has been described in detail by Griffiths (822).

GENUS DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Punica.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Griffiths 822.

(ii) *On Wood Structure*

Bailey 78, Greguss 2522, Record 1843, 1851.

143. SONNERATIACEAE

(FIG. 149 on p. 662)

SUMMARY

(i) GENERAL

Trees. Some of the species of *Sonneratia* inhabiting Mangrove Swamps from Africa to Australia are provided with **vertical branches of the root system** projecting into the air or water above the mud. The occurrence of **intraxylary phloem** in both *Duabanga* and *Sonneratia* is also noteworthy.

(ii) WOOD

Vessels medium-sized to moderately small, mostly in multiples of 2 or 3 cells, perforations simple, intervacular pitting alternate and moderately small to large, vested, pits to ray cells either similar or large and simple, members of medium length. **Parenchyma** absent or vasicentric. **Rays** exclusively uniseriate or up to 2 cells wide, homogeneous or heterogeneous. **Fibres** with simple pits, septate in *Sonneratia*, of medium length to moderately short.

LEAF

Isobilateral in *Sonneratia apetala* Ham. Upper **epidermis** provided with cuticular ridges, and the lower with papillae in *Duabanga*. **Cork warts** recorded in certain species of *Sonneratia*. **Stomata** deeply sunken and present on both surfaces in *Sonneratia acida* Linn.; rubiaceous and equally numerous on both surfaces in *S. apetala* Ham. **Mesophyll** including numerous large mucilage cells, the central portion consisting of aqueous tissue containing branched sclerenchymatous idioblasts.

AXIS

STEM

Young stem of *Duabanga* and *Sonneratia* provided with collenchymatous wings. **Cork** arising in the sub-epidermis in *Sonneratia apetala* Ham. Primary **cortex** of *Sonneratia* mostly consisting of spongy parenchyma, outer part containing branched sclerenchymatous idioblasts. **Xylem** in the form of a continuous cylinder traversed by narrow rays. Vessels with simple perforations. **Phloem** including sclerenchyma. **Pith** supported by sclerenchymatous elements, more conspicuous in *Duabanga* than in *Sonneratia*; composed of pitted cells and distinctly lacunar in *Sonneratia apetala* according to Mullan (1571). **Intraxylary phloem** present; that of *Sonneratia apetala* containing a few fibres and crystal cells. **Secretory cells** occur in the phloem (including the intraxylary phloem) of *S. apetala*, and, according to Mullan (1571), **crystals** in vertical rows of special cells in the secondary phloem of the same species.

WOOD (Fig. 149 A-D)

Vessels medium-sized (100–200 μ mean tangential diameter); solitary and in numerous multiples of 2 or 3 cells, occasionally with a tendency to form loose oblique or tangential lines; 2–10 per sq. mm. in *Duabanga*, usually about 20 per sq. mm. in *Sonneratia*. Perforations simple. Intervascular pitting alternate, large in *Duabanga*, medium-sized to rather small in *Sonneratia*; pits to ray cells often large and simple in *Duabanga*, mostly similar to the intervacular pitting in *Sonneratia*, but with a few larger pits or with 2 pits subtending 1 large ray pit; vestured (78). Tyloses often present, occasionally sclerosed in *Sonneratia* (1649). Mean member length in *Sonneratia* 0.4–0.5 mm. and in *Duabanga* 0.6–0.8 mm. **Parenchyma** absent from *Sonneratia*; paratracheal in *Duabanga*, as narrow to rather wide vasicentric sheaths round the vessels (Fig. 149 A) and occasionally linking adjacent vessels. **Rays** exclusively uniseriate, except for occasional biseriate parts, in *Sonneratia*; more commonly 2 and occasionally 3 cells wide, in *Duabanga*, though predominantly uniseriate in some specimens; commonly about 1 mm. high in the latter, shorter in *Sonneratia*; 10–18 per mm.; in *Sonneratia* composed almost entirely of procumbent cells, apart from rows of crystalliferous cells (Kribs's Homogeneous Type III); in *Duabanga* heterogeneous, with up to about 10 marginal rows of square or upright cells, the uniseriates composed of upright and procumbent cells. Cells of *Sonneratia* often filled with a dark, gum-like substance and interspersed with rows of square cells, each cell containing a solitary crystal. **Fibres** with simple pits; pits mostly on the radial walls and rather few in *Duabanga*, but numerous in *Sonneratia*. Septate in *Sonneratia*. H. P. Brown (1679) states that there is only 1 septum per fibre in the Indian species; this is not so in other species. Walls thin in *Duabanga*, moderately thick in *Sonneratia*. Mean length in *Sonneratia* 0.7–1.0 and in *Duabanga* 1.2–1.4 mm. Janssonius (1154) notes a distinct type of fibre round the vessels in *Sonneratia*; this is distinguished by being shorter, and having rounded, untapered ends, thinner walls, and intercellular spaces; Brown (1679), however, doubts if such a distinction can be drawn in the Indian species; some markedly shorter fibres with blunt ends can be distinguished in *Duabanga sonneratioides* Buch-Ham.

Root

The following particulars concerning the structure of the vertical, negatively

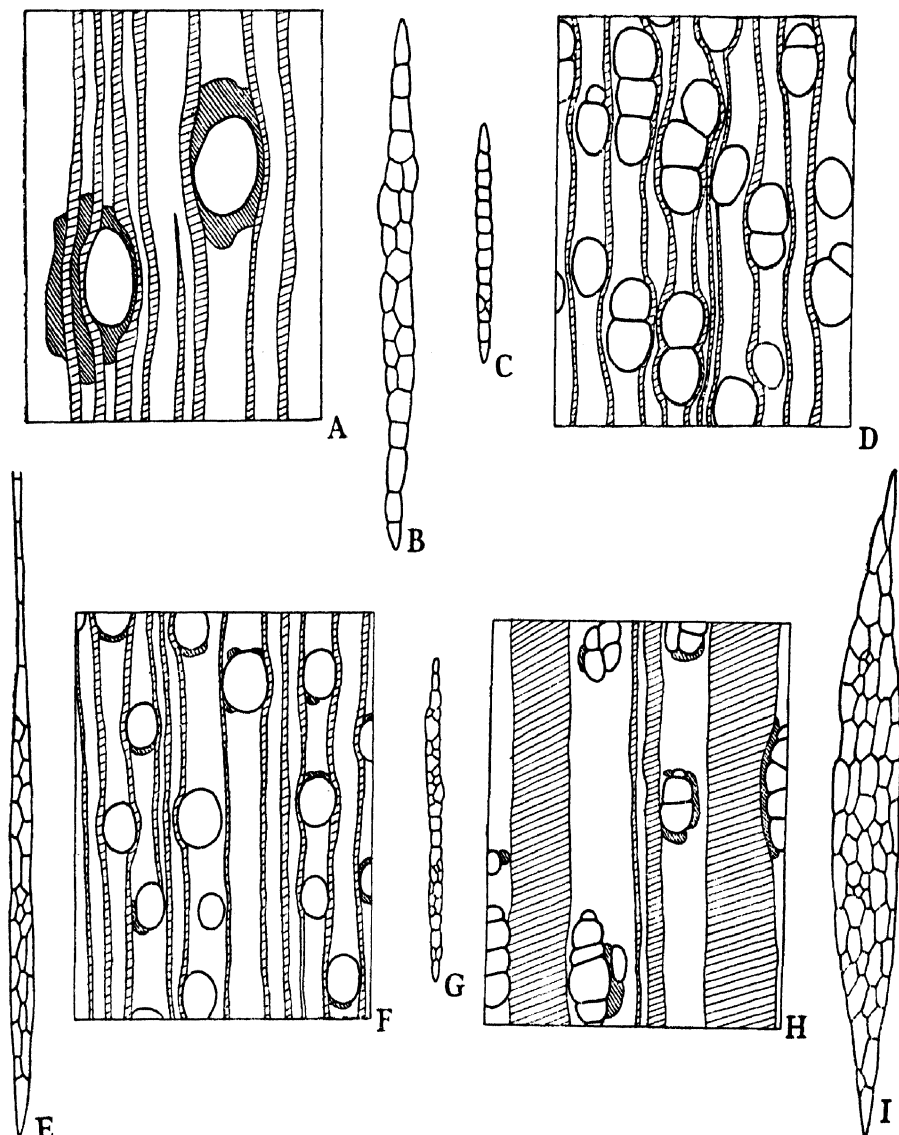


FIG. 149. SONNERATIACEAE, A-D; ONAGRACEAE, E-I

A, *Duabanga sonneratioides* Buch-Ham. B, *D. sonneratioides* Buch-Ham. C, *Sonneratia apetala* Ham. D, *S. apetala* Ham. E, *Jussiaea latifolia* Benth. F, *J. latifolia* Benth. G, *Oenothera biennis* Linn. H, *Fuchsia riccartonii* Hort. I, *F. macrostemma* Ruiz. et Pav.

geotropic portions of the root system ('pneumatophores') of *Sonneratia apetala* Ham. have been recorded by Mullan (1571):

Cork consisting of a succession of lamellae each composed of 3 layers of

cells. Cells of the outer layer of cork rounded externally and not suberized; cells of the middle layer tabular and suberized; those of the inner layer radially elongated, rounded on the inside and suberized. Two layers of approximately spherical cells, present between each succeeding cork lamella, facilitate separation at these points. **Cortex**, at the distal end of the 'pneumatophore', composed of rounded cells interspersed with schizogenous, intercellular spaces; also containing crystalliferous cells and branched sclerenchymatous idioblasts, the latter less numerous away from the distal end. Cortex at the proximal end of the root similar in structure to that of the subterranean root and supported by curved, lignified spicules. **Phloem** including isolated strands of fibres and vertical rows of crystalliferous cells. **Xylem** in the form of a broad feebly lignified ring. **Pith** containing sclerenchymatous idioblasts at the distal but not at the proximal end.

Earlier accounts of the structure of the 'pneumatophores' of *Sonneratia* by Liebau (1368) and Emould (627) agree for the most part with that by Mullan. Liebau failed to observe the S-shaped, spring-like cells previously described by Westermaier from the cortex of the lower part of the 'pneumatophores' and terrestrial roots. These are, however, probably identical with the 'curved, lignified spicules' observed by Mullan. Liebau thought that the vascular structure of the 'pneumatophore' resembles that of a stem rather than a root, especially as the smallest vessels are those towards the centre of the axis, whilst the phloem and xylem elements often occur along the same radii.

The spongy aerial roots of *Sonneratia* have, for many years, been regarded as 'breathing' organs which serve for the intake of oxygen and liberation of carbon dioxide, which would otherwise be difficult in roots growing in the peculiar substratum in the muddy swamps of tropical estuaries. More recently, however, Troll (2282) and Troll and Dragendorff (2283), whose work was reviewed by Metcalfe (1494 A), have shown how the unusual root system enables a succession of fibrous absorbing roots to be formed at progressively higher levels on the negatively geotropic roots. This occurs at intervals as the level of the muddy substratum is raised, owing to the deposition of colloidal matter suspended in the water. Troll pointed out, however, that the importance of the aerial roots in performing this function does not exclude the possibility of their serving for gaseous exchange as well.

The **terrestrial roots** of the same species exhibit the following features. Cortex lacunar; component cells mostly triradiate, and supported by thickening ridges and by vertically elongated cells with thick, pitted, but unlignified walls. Cork arising superficially.

TAXONOMIC NOTES

The wood structure of *Duabanga* and *Sonneratia* differs considerably in respect of the vessels, parenchyma, rays, and fibres. If these were the sole taxonomic criteria it would appear doubtful if these genera should be included in the same family. The general anatomy of *Duabanga* is not so well known as that of *Sonneratia*, but here there are points in common between the 2 genera, notably the occurrence of intraxylary phloem. This character also serves to connect the Sonneratiaceae with the Lythraceae in which they were included in the Bentham and Hooker system.

ECONOMIC USES

Both *Duabanga* and *Sonneratia* furnish good packing-case timbers, which are in demand in some localities in India.

GENERA DESCRIBED

FOR GENERAL ANATOMY AND WOOD STRUCTURE

Duabanga, *Sonneratia*.

LITERATURE

(i) *On General Anatomy*

Emould 627, Liebau 1368, Metcalfe 1494, 1494 A, Mullan 1571, Troll 2282, Troll and Dragendorff 2283.

(ii) *On Wood Structure*

Bailey 78, den Berger 179, 182, Foxworthy 705, Howard 1088, Janssonius 1154, Kanehira 1206, Panshin 1649, Pearson and Brown 1679, Record 1843, 1851.

144. ONAGRACEAE

(FIG. 148 on p. 658; FIG. 149 on p. 662; FIG. 150 on p. 666)

SUMMARY

(i) GENERAL

A temperate and sub-tropical family consisting mainly of herbs but including some shrubs. The occurrence of **intraxylary phloem** in the axis provides one of the most important diagnostic features, and is indicative of affinities with the Lythraceae and other related families. **Interxylary phloem** has also been recorded in a few genera. The **hairs** are nearly all simple and include unicellular and uniseriate types. The **stomata** are surrounded by 3 or more subsidiary cells, sometimes resembling those of the Cruciferae. The **mesophyll** is dorsiventral or centric, and the spongy and palisade portions not always clearly differentiated. **Raphides** are common in most genera. Sclerenchyma is generally poorly developed or absent from the **veins**. There is a principal arc-shaped vascular strand in the **petiole**, sometimes accompanied by lateral accessory strands. The **cork**, which often includes phelloid cells, the latter sometimes in layers alternating with the suberized cells, is usually deep-seated in origin. It is sometimes replaced by **aerenchyma** in species from marshy habitats, e.g. in *Epilobium* and *Jussiaea*.

(ii) WOOD

Vessels small to moderately small, often with numerous radial multiples and clusters, perforations simple, intervacular pitting alternate, pits to parenchyma simple and often elongated; members of medium length to moderately short. **Parenchyma** paratracheal, scanty. **Rays** 2-9 cells wide, commonly more than 1 mm. high, heterogeneous, composed almost entirely of square or upright cells except in *Oenothera*. **Fibres** with simple pits, usually septate, moderately short. **Included phloem** of the 'foraminate' type occasionally present.

LEAF

Dorsiventral or centric, the spongy and palisade mesophyll not always

distinct. **Hairs** nearly always simple, commonly with granular or verrucose surfaces; unicellular of various shapes, often club-shaped, e.g. in species of *Clarkia* and *Oenothera*; short, uniseriate in species of *Fuchsia*, *Jussiaea*, *Ludwigia*, long uniseriate in *Trapa bispinosa* Roxb. according to Sabnis (1977). Leveillé (1365) found the structure of the hairs to be valuable in classifying species of *Oenothera*. **Epidermis** including mucilaginous cells in species of *Jussiaea* and *Trapa*. **Stomata** surrounded by 3 or more subsidiary cells, the latter sometimes consisting of 2 large and 1 small cells as in the Cruciferae; occurring on both surfaces or confined to the lower side in most species, but limited to the upper surface in *Epilobium crassum* Hook. f. and in *Trapa bispinosa* Roxb. according to Sabnis (1977). Sclerenchyma said to be generally absent from the **veins** except in certain species of *Fuchsia*. **Petiole** (Fig. 148 G), in transverse sections through the distal end of all investigated species, exhibiting a single, usually flattened, arc-shaped, vascular strand, sometimes accompanied by lateral accessory strands. Betts (188) refers to **canals** surrounded by epithelium occurring at intervals in the mesophyll of *Epilobium pedunculare* Hook. f. and *E. pubens* A. Rich. **Crystals**. Raphides, usually situated in sacs and sometimes embedded in or replaced by mucilage, recorded or observed in *Circaea*, *Clarkia*, *Epilobium*, *Eucharidium*, *Fuchsia*, *Gaura*, *Gayophytum*, *Gongylocarpus*, *Hauya*, *Jussiaea*, *Lavauxia*, *Lopezia*, *Ludwigia*, *Megapterium*, *Oenothera*, *Zauschneria*. Raphides accompanied by clustered crystals in *Jussiaea* and *Ludwigia*. Crystals said to be exclusively clustered in *Trapa*. Styloids recorded in a species of *Hauya*. **Oil cells** recorded by Stein (2192) in the epidermis of *Ludwigia alternifolia* Linn. and less regularly in species of *Circaea*, *Clarkia*, *Fuchsia*, *Gaura*, *Jussiaea*, *Oenothera*, *Trapa*.

AXIS

STEM (Fig. 148 H and J)

Cork arising in the pericycle of *Clarkia* as well as in all of the genera and species represented in the Kew slide collection, and probably in others as well; often including phelloid cells, the latter sometimes arranged in layers alternating with the suberized cells. Cork often replaced by **aerenchyma** (Fig. 150 A-C) in submerged portions of stems and also in the roots of species inhabiting marshes, notably in *Epilobium* and *Jussiaea*. Primary **cortex** provided with well-developed intercellular spaces in species of *Fuchsia*, *Jussiaea*, *Ludwigia*, *Oenothera*. **Endodermis** in *Epilobium pedunculare* Hook. f. and *E. pubens* A. Rich. described by Betts (188) as well defined and consisting of a single layer of large cells with suberized walls. **Pericycle** usually containing isolated strands or, less frequently, a continuous ring of fibres in species of *Circaea*, *Clarkia*, *Epilobium*, *Fuchsia* (none seen in the specimen illustrated in Fig. 148 H), *Gaura*, *Gayophytum*, *Godetia*, *Gongylocarpus*, *Jussiaea*, *Kneiffia*, *Lavauxia*, *Lopezia*, *Ludwigia*, *Megapterium*, *Oenothera*, *Raimannia*, *Zauschneria*. **Phloem** reported as sometimes containing stone cells in *Hauya* and fibres in *Fuchsia*. **Xylem** forming a continuous cylinder traversed by narrow rays in all of the species represented in the Kew slide collection. Vessels with simple perforations; occasional multiperforate plates also recorded (see 'Wood'). **Pith** often becoming hollow; including large intercellular spaces in *Trapa*. **Intraxylary phloem**, which is one of the most important diagnostic features for the family, has been recorded in numerous species of *Circaea*,

Clarkia, *Epilobium*, *Eucharidium*, *Fuchsia*, *Gaura*, *Gayophytum*, *Godetia*, *Gongylocarpus*, *Hauya*, *Jussiaea*, *Kneiffia*, *Lavauxia*, *Ludwigia*, *Megapterium*, *Oenothera* (Fig. 148 J), *Raimannia*, *Trapa*, *Zauschneria* and probably occurs throughout the family. It adjoins the vascular bundles in some species, but forms isolated strands in the pith of others. For **interxylary phloem** see

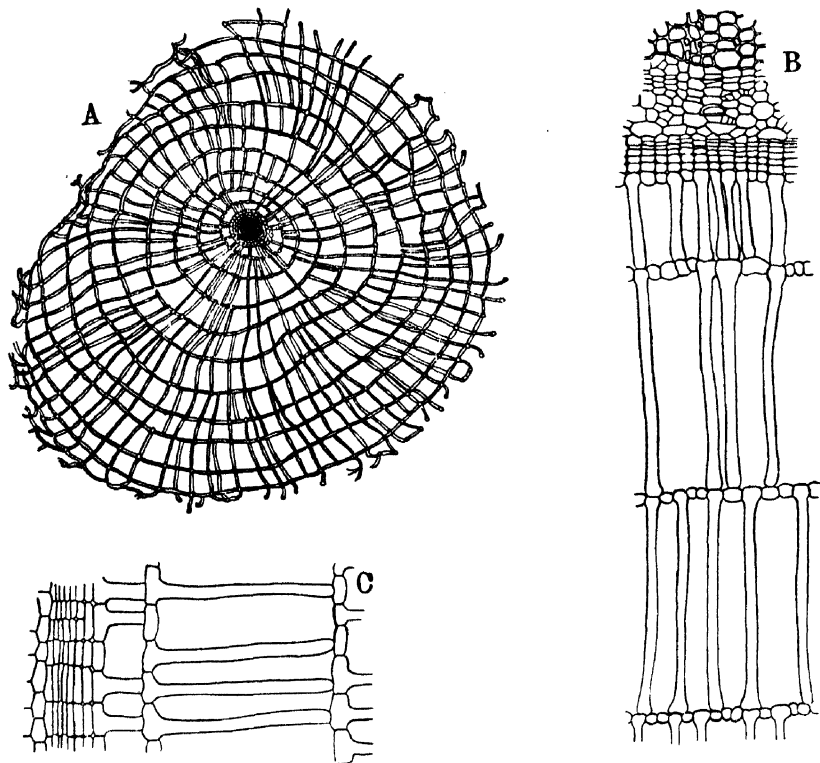


FIG. 150. ONAGRACEAE

A, Cross-section through an aerial root of *Jussiaea repens* Linn. B, C, *Jussiaea peruviana* L.: B, cross-section; C, radial longitudinal section of the aerenchyma.—A, after Goebel, B, C, after H. Schenck.

under 'Anomalous Structure', p. 667. **Crystals** occur chiefly in the form of raphides, which are present in varying abundance in different genera and species; and have been observed at Kew in species of *Epilobium*, *Fuchsia*, *Kneiffia*, *Lavauxia*, *Megapterium*, *Raimannia*. Raphides sometimes embedded in or replaced by mucilage. **Oil cells** recorded by Stein (2192) in the epidermis of *Ludwigia alternifolia* Linn. and less regularly in species of *Circaea*, *Clarkia*, *Fuchsia*, *Gaura*, *Jussiaea*, *Oenothera*, *Trapa*.

WOOD (Fig. 149 E-I)

Vessels very small to moderately small (25–100 μ mean tangential diameter); solitary and in numerous radial multiples and irregular clusters of several cells except in *Jussiaea*; 7–25 per sq. mm. Perforations simple; according to Solereder, Grosse mentions the occurrence of a few multiperforate

plates in the herbaceous stems of species of *Godetia* and *Oenothera*. Intervascular pitting alternate, moderately small, vested (1886); pits to ray or wood parenchyma usually simple, similar in shape to the intervascular pitting or elongated, sometimes almost scalariform. Tyloses sometimes present. Mean length 0.3–0.5 mm. **Parenchyma** sparse, limited to a few cells round the vessels. **Rays** 2–3 cells wide in *Jussiaea* and *Oenothera* and occasional specimens of *Fuchsia*, up to 9 cells wide in some specimens or species of *Fuchsia*, e.g. *F. riccartoni* Hort., and with low uniseriate rays; uniseriate rays high and numerous in the other genera; uniseriates typically composed of upright cells only, but of upright and procumbent cells in *Oenothera*; commonly more than 1 mm. high, except in *Oenothera* mostly 10–16 rays per mm., rather fewer in some species of *Fuchsia*; heterogeneous in *Oenothera*; composed almost entirely of large square or upright cells in *Fuchsia* and *Jussiaea*; with sheath cells, except in *Oenothera*. Gum and crystals not observed, but numerous large crystals reported (1886) in *Jussiaea latifolia* Benth. **Fibres** with very small simple pits, very numerous on the radial walls in *Fuchsia*; septate in most species of *Fuchsia* and *Jussiaea*; walls thin; mean length 0.7–0.8 mm. **Included (interxylary) phloem** of the 'foraminate' type, with strands of included phloem scattered in a normal xylem, reported by Record (1851) in *Epilobium* and *Oenothera*; the strands sometimes grouped in tangential rows in *Oenothera* (see also under 'Anomalous Structure' below).

ROOT

Aerenchyma (Fig. 150 A–C) present in portions of the root system of *Jussiaea* above ground-level. Lateral roots of *Trapa* each provided with one, poorly developed strand of phloem and xylem.

ANOMALOUS STRUCTURE

Interxylary phloem present in the stem and/or root of various species of *Epilobium*, *Gaura*, *Lopezia*, *Oenothera* (see also under 'Wood' above). Interxylary periderm described by Moss (1564) as occurring in the perennating organs of *Epilobium angustifolium* Linn., where it is formed 'each year over the surface of the wood connected with the previous year's aerial shoots and joins with external periderm in the basal region of each of these decadent shoots'. The interxylary periderm is produced by a phellogen which arises in a parenchymatous zone of the xylem. The ability of the perennating organs to withstand adverse conditions is thought to be correlated with the presence of interxylary periderm.

ECONOMIC USES

The fruits of species of *Trapa* are known as Water Chestnuts, and the seeds from them are ground into flour and used in various parts of the world (e.g. China, India, Tropical Africa) to make bread. Species of *Clarkia*, *Fuchsia*, *Godetia*, *Oenothera*, &c., are commonly cultivated for ornamental purposes.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Chamaenerion, *Circaea*, *Clarkia*, *Epilobium*,* *Eucharidium*, *Fuchsia*,*

Gaura, *Gayophytum*, *Godetia*,* *Gongylocarpus*, *Hauya*, *Isnardia*, *Jussiaea*, *Kneiffia*,* *Lavauxia*,* *Lopezia*, *Ludwigia*, *Megapterium*,* *Oenothera*,* *Oocarpon*, *Raimannia*,* *Trapa*.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(*Epilobium*), *Fuchsia*, (*Godetia*), *Jussiaea*, *Oenothera*.

LITERATURE

(i) *On General Anatomy*

Betts 188, Gates 750, Leveillé 1365, Moss 1564, Sabnis 1977, Stein 2192.

(ii) *On Wood Structure*

Record 1843, 1851, Record and Hess 1886, Williams 2430.

145. LOASACEAE

(FIG. 148 on p. 658; FIG. 151 on p. 670)

SUMMARY

A family occurring mainly in tropical and temperate parts of the New World. Members are mostly herbaceous or, more rarely, woody; provided on both leaf and stem with a wide variety of characteristic **hairs**, some of which possess powerful stinging properties, owing to the presence of an irritant substance in the hairs themselves or the surrounding basal cells. The irritant substance is readily liberated because the hairs are brittle. **Cystoliths** are common in the hairs. The stem of herbaceous species contains a ring of collateral **vascular bundles** and the woody species a cylinder of xylem, whilst intermediate types also occur. Mechanical tissue in herbaceous species is chiefly in the form of collenchyma in the outer part of the cortex, but it is frequently interrupted by groups of chlorenchyma extending outwards to the epidermis. In living material the chlorenchyma patches can often be seen with the naked eye as dark-green spots or streaks on the stem surface.

LEAF

Centric. **Hairs** (Fig. 151) include the following and intermediate types.

A. *Unicellular*

(i) Simple, of variable length, with silicified or non-silicified walls. (ii) Conical, pointed, strongly silicified, the surface beset with downwardly directed spines. (iii) Strongly silicified and barbed, comparable with a many-fluted anchor (Fig. 151 A-C), the stalk sometimes covered with curved spines as well. (iv) Hooked or sickle-shaped, and provided with a multicellular base. (v) Filiform, with local tuberculous swellings, sharply attenuated and sometimes barbed at the apex. (vi) Elongated, silicified stinging hairs often with slightly recurved, blunt, or capitate apices; filled with a yellowish irritant substance, readily liberated owing to the brittleness of the hair and causing serious injury if discharged into the skin of animals.

B. *Multicellular*

(i) Glandular, with uniseriate stalks and uniseriate heads. Lime or silica frequently present in structures resembling **cystoliths** (Fig. 151 D-G) situated in the hairs themselves or cells at their bases in species of *Blumenbachia*, *Caiophora*, *Eucnide*, *Gronovia*, *Loasa*, *Mentzelia*, *Petalonyx*; these bodies are stated to suggest affinities between the Loasaceae and Cucurbitaceae. **Stomata** ranunculaceous in *Blumenbachia*, *Caiophora*, *Eucnide*, *Mentzelia*, *Petalonyx*; confined to the lower surface in the dorsiventral leaves of *Caiophora* and *Eucnide*, but on both sides in the isobilateral leaf of *Petalonyx thurberi* A. Gray. The **mesophyll** of this last species contains a free network of tracheids, and lignified pitted cells above and below the midrib. Transverse sections through the distal end of the **petiole** exhibit a slightly crescent-shaped vascular strand accompanied by smaller accessory bundles in the wings in *Blumenbachia hieronymi* Urb. (Fig. 148 F); a dorsally flattened, somewhat interrupted cylindrical strand, accompanied by 2 medullary bundles and others in the wings, observed in the corresponding position in *Loasa vulcanica* Andre (Fig. 148 I).

AXIS

STEM (Fig. 148 E and K)

Outer part of the **cortex** of herbaceous species provided with a well-developed but interrupted ring of chlorenchyma, extending outwards to the epidermis. **Cork** examined only in *Mentzelia*, originating there on the inside of the pericyclic fibres. **Pericycle** containing yellow, vertically elongated groups of thickened parenchymatous cells in *Petalonyx*; a few scattered fibres seen in *Loasa vulcanica* Andre. Herbaceous species provided with a somewhat interrupted **vascular ring** (Fig. 148 E), but a cylinder of **xylem** occurs in woody members of the family, e.g. in species of *Mentzelia* and *Petalonyx*. Intermediate types of vascular structure also occur, e.g. in *Loasa vulcanica* (Fig. 148 K). The xylem includes fairly wide vessels with simple perforations; wood fibres with fairly wide lumina and simple and/or bordered pits.

GENERA DESCRIBED

Blumenbachia,* *Caiophora*, *Eucnide*, *Gronovia*, *Loasa*,* *Mentzelia*, *Petalonyx*.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy
Gilg 776.

146. TURNERACEAE

(FIG. 152 on p. 672; FIG. 154 on p. 682)

SUMMARY

(i) GENERAL

A small, mainly tropical American family of herbs of which some tend to be shrubby. A very detailed account of the anatomy of the family was pub-

lished by Berger (184), from whose thesis a large part of the present description has been taken. The diverse kinds of **hairs** are of considerable taxonomic value, whilst the occasional occurrence of scalariform perforations plates in the vessels in the neighbourhood of the primary wood of the axis is noteworthy.

(ii) WOOD

Vessels very small to medium-sized, with numerous multiples, perforations simple or simple and scalariform, intervacular pitting alternate and very

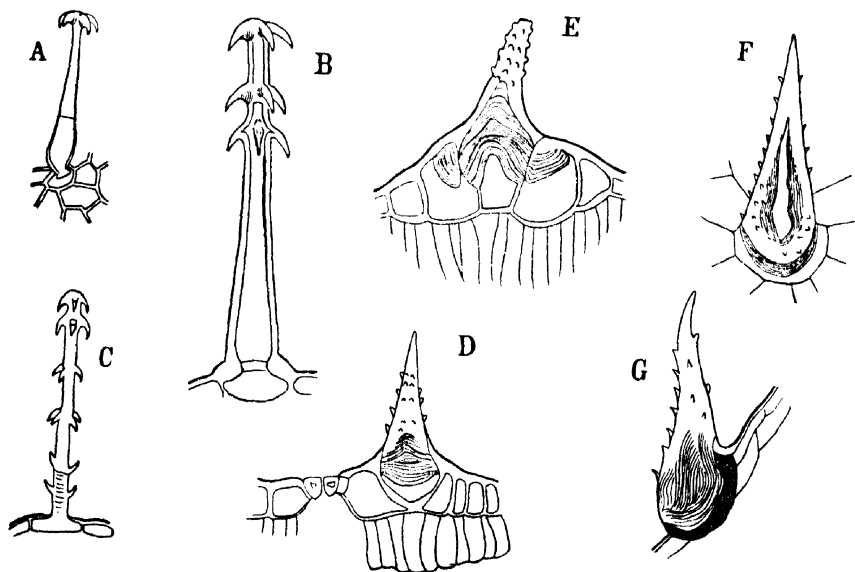


FIG. 151. LOASACEAE

A-C, Unicellular anchor-hairs. A, B, *Eucnide lobata* Gray; C, *Caiophora lateritia* (Hook.) Klotzsch. D, E, *Petalonyx thurberi* Gray; D, cystolith-hair; E, trichome with merely calcified, but strongly thickened wall, without a cystolith, but with cystoliths in the subsidiary cells. F, G, *Loasa chelidoniifolia* Benth.; F, cystolith hair adpressed to the leaf, back-view; G, in side-view.—By Solereder.

small. **Parenchyma** apotracheal, diffuse or reticulate. **Rays** up to 5 cells wide, heterogeneous or composed entirely of square and upright cells. **Fibres** with numerous indistinctly to distinctly bordered pits.

LEAF

Generally dorsiventral, with 1 or 2 layers of palisade tissue in different species; isobilateral, with a single layer of palisade cells towards both surfaces in *Streptopetalum hildebrandti* Urban, *Turnera diffusa* Willd. and the variety *aphrodisiaca* Urban, *T. hermannioides* Cambess, and *T. ulmifolia* Linn. **Hairs** include the following diverse types.

A. Non-glandular

(i) Simple, unicellular, usually with thick sclerified walls and narrow lumina in species of *Erblichia*, *Mathurina*, *Piriqueta*, *Turnera*, *Wormskioldia*. (ii) Simple, uniseriate, with thin or thick walls in species of *Hyalocalyx*, *Piriqueta*,

Turnera; uniseriate hairs, sometimes covered with fine granulations, in species of *Hyalocalyx*, *Streptopetalum*, *Turnera*. (iii) Various types of stellate hair recorded, especially in *Piriqueta* (section *Eupiriqueta*), but also occurring in a few species of *Streptopetalum*, *Turnera*, *Wormskioldia*. Variations in the type of stellate hair are valuable for the identification of species.

B. Glandular

(i) Each having a short multicellular stalk, bearing a very large, spherical, terminal cell in species of *Hyalocalyx* and *Turnera*. (ii) Similar to (i) but pluricellular and somewhat resembling a mulberry fruit in *Erblichia* and numerous species of *Turnera*. These glands appear very different in fresh and dried material respectively. Similar glandular hairs occur in the Labiatae and Chenopodiaceae. (iii) Clavate hairs with a uniseriate base and multicellular head, recorded, especially on the lower surface of the leaf, in species of *Piriqueta* and *Turnera*. (iv) Multicellular hairs each with a massive base, but tapering to a biseriate to triseriate distal end, the terminal cell being spherical, recorded in a few species of *Piriqueta*, *Streptopetalum* (Fig. 152 A), *Turnera*, *Wormskioldia*. Glands each having a short peduncle, traversed longitudinally by a vascular strand and provided with a head which is at first concave and resembles a small *Peziza* fructification, but later becomes convex at the onset of secretion, recorded at the base and margins of some of the leaves in species of *Mathurina*, *Piriqueta*, *Turnera* (Fig. 152 B), *Wormskioldia*. Disks of the glands composed of palisade cells containing a granular material readily stained by Sudan III.

Epidermis sometimes containing mucilage, e.g. in *Piriqueta*, *Streptopetalum*, and certain species of *Turnera*. Cells of the upper usually with less sinuous anticlinal walls than those of the lower epidermis. **Stomata** confined to the lower surface in certain species of *Mathurina*, *Piriqueta*, *Streptopetalum*, *Turnera*, *Wormskioldia*, but recorded on both surfaces in other species of *Piriqueta*, *Streptopetalum*, *Turnera*, *Wormskioldia*; mostly rubiaceous, but sometimes cruciferous and ranunculaceous; all 3 types known to occur together in a single leaf, e.g. in *Turnera diffusa* Willd. var. *aphrodisiaca* Urban. **Mesophyll** containing sclerenchymatous idioblasts in *Turnera hilaireana* Urban. **Petiole**, in transverse sections through the middle portion, exhibiting, according to Berger (l.c.), a solitary, more or less open, arc-shaped vascular strand in species of *Turnera* and *Wormskioldia*. A slightly crescent-shaped abaxial vascular strand accompanied by a smaller adaxial one, the xylem groups of both being directed towards one another, observed at Kew in sections through the distal end of the petiole of *T. ulmifolia* Linn. (Fig. 154 G). An arc of 3 separate bundles, the median one much larger than the other 2, recorded in species of *Erblichia*, *Mathurina*, *Wormskioldia*, and a closed circular strand in *Piriqueta*. Very small, clustered **crystals** frequent in the spongy mesophyll and, less often, in the palisade tissue. **Secretory elements** known to occur only in the form of fairly frequent tanniniferous idioblasts.

AXIS

STEM (Fig. 154 I)

Young stem usually provided with **hairs** of the same types as those described for the leaf. **Cork** arising in the sub-epidermis in certain species

of *Turnera*. **Cortex** varying considerably in width; usually consisting mainly or wholly of collenchyma. Isolated, rounded fibres recorded immediately below the epidermis in *Turnera hilaireana* Urban. **Pericycle** including a continuous ring of sclerenchyma, an interrupted ring of fibre strands, a circle of solitary fibres, or entirely devoid of sclerenchyma according to the species. **Phloem** always devoid of sclerenchyma; present in the form of a continuous cylinder, cylindrical strands, or scattered sieve tubes. **Xylem** nearly always

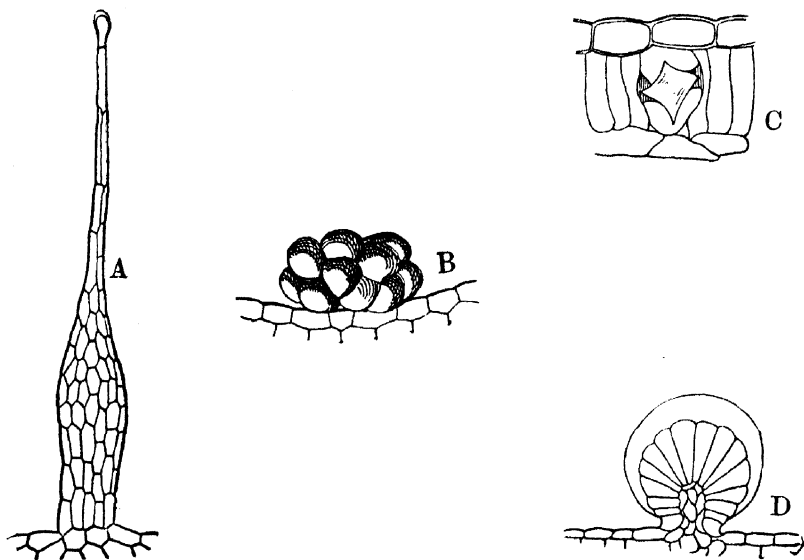


FIG. 152. TURNERACEAE, A-B; PASSIFLORACEAE, C-D

A, Glandular shaggy hair of *Streptopetalum hildebrandtii* Urb. B, Glands of *Turnera annularis* Urb. C, Crystal-cell from the palisade-tissue of *Adenia lobata* (Jacq.) Engl. D, Glandular shaggy hair of *Passiflora clathrata* Mast. in longitudinal section.—A-C by Solereder, D after Harms.

forming a continuous, fairly thick cylinder traversed by narrow rays. Vessels small (up to about $45\ \mu$ in radial diameter in *Turnera ulmifolia* Linn.), usually irregularly distributed but more rarely in radial rows; perforations mostly simple apart from occasional scalariform plates with a few bars recorded in the region of the primary xylem in *Piriqueta* and *Turnera*. Ground-mass of the wood consisting of fibres with small pits, the latter described as distinctly bordered in at least certain species. Wood parenchyma scanty. Rays usually 1 or 2 cells wide, recorded by Berger as up to 5 cells wide in certain species of *Turnera*. Wide rays have been recorded by Colozza (455) in *Streptopetalum* and *Wormskioldia*. Leaf trace bundles sometimes traverse the cortex longitudinally for a considerable distance and constitute **cortical vascular bundles** (Fig. 154 1). **Pith** generally composed of cells with cellulose walls, but the outer part thickened in some species, and islands of sclerosed pitted cells recorded in the centre of the pith in *Turnera hilaireana*. Pitted cells also noted in the pith of *Streptopetalum* and other species of *Turnera*. Clustered **crystals** usually plentiful in unligified tissues, especially in the cortex and pith. **Secretory elements** known to occur only in the form of thick-walled, tanniniferous

idioblasts, frequently arranged in longitudinal columns, the transverse walls sometimes breaking down; recorded in the pith and, less frequently, in the cortex and phloem of a few species of *Piriqueta* and *Turnera*, but not present in numerous other species of *Turnera*.

WOOD¹

Erblichia

Vessels small to medium-sized, in multiples of 2–6 cells. Perforations simple. Intervascular pitting alternate, very small. **Parenchyma** apotracheal, in fine reticulate lines. **Rays** up to 5 cells wide, markedly heterogeneous. **Fibres** with numerous indistinctly bordered pits and thick walls.

Turnera

Vessels very small, solitary, and in short to long multiples; with spiral thickening. Perforation plates simple and scalariform with numerous fine bars. Intervascular pitting alternate and very small; pits to ray cells often elongated and scalariform. **Parenchyma** apotracheal, diffuse. **Rays** up to 4 cells wide; very numerous; composed almost entirely of square and upright cells. **Fibres** with numerous, very small, distinctly bordered pits; walls thick.

ROOT

Cork poorly developed. **Cortex** composed of homogeneous parenchyma. **Endodermis** not clearly differentiated. **Pericycle** sometimes including fibres. **Xylem** forming a thick, compact cylinder composed of tracheids, vessels with spiral thickening or scalariform pitting or with ovoid pits with linear apertures. **Crystals** said to be absent. Berger noted little difference in the structure of the secondary xylem in different genera and species.

TAXONOMIC NOTES

It is generally thought by systematists that the Turneraceae have close affinities with the Passifloraceae, a view which is supported by the anatomical similarity of the 2 families. Berger (184) has pointed out that *Streptopetalum* and *Wormskioldia* are indistinguishable by means of their anatomical features.

Taylor (2237) states that a cursory examination of the wood gives an indication that this family belongs to the Flacourtiaceae complex. It should, however, be noted that the 2 most characteristic features of the Flacourtiaceae—septate fibres and parenchyma absent or paratracheal only—are lacking from the Turneraceae.

ECONOMIC USES

The dried leaves of *Turnera diffusa* Willd. var. *aphrodisiaca* Urban constitute the drug Damiana, to which aphrodisiac and mild purgative properties have been attributed. Important microscopical characters of this material include: the isobilateral mesophyll; the unicellular, thick-walled, warty trichomes; the glandular hairs with short, unicellular stalks and few-celled head sometimes containing reddish-brown material; the numerous, mostly rubiaceous and cruciferous, but occasionally ranunculaceous stomata confined to the lower surface; the petiole with an open arc-shaped vascular strand

¹ Based entirely on the description by Record and Hess (1886).

containing small, radially arranged vessels in the xylem, the strand being supported by thick-walled fibres in the pericyclic region; the yellowish material secreted in the midrib and some of the epidermal cells; the mostly clustered and occasional solitary crystals of calcium oxalate.

GENERA DESCRIBED

Erblichia, Hyalocalyx, Mathurina, Piriqueta, Streptopetalum, Turnera,* Wormskioldia.

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Berger 184, Colozza 455, Gilg 775.

(ii) *On Wood Structure*

Record 1851, 1885, Record and Hess 1886, Taylor 2237.

147. PASSIFLORACEAE

(FIG. 152 on p. 672; FIG. 153 on p. 676; FIG. 154 on p. 682)

SUMMARY

(i) GENERAL

A tropical and sub-tropical family of very varied habit including many climbers, but others are more woody and have the form of shrubs or small trees. *Adenia* includes xerophytic species such as *A. pechuelii* (Engl.) Harms which occur in the driest regions of Africa. In this and closely related species the plant consists of a collection of short, fleshy, tuberous stems from which erect or ascendant, sometimes thorny branches arise. Other species of *Adenia* possess a single, partly or wholly subterranean, napiform tuber bearing somewhat woody climbing stems. *A. venenata* Forsk. (syn. *Modecca abyssinica* Hochst.) is a succulent species. The **leaf** is usually dorsiventral, but exhibits isobilateral structure in some genera. Sessile or shortly stalked **glands** are common in the petiole, and glandular spots less frequent on the lower side of the lamina. The **hairs** are mostly unicellular or uniseriate, but glandular shaggy types also occur in *Passiflora*. The leaf **epidermis** is sometimes 2-layered. The **stomata**, usually confined to the lower surface, are ranunculaceous. **Crystals**, where present, are solitary rhombohedra or clustered. **Secretory elements** include tanniferous cells which are common in the parenchymatous portion of both stem and leaf, whilst secretory cavities, which also contain tannin, have been recorded in the leaf and axis of *Adenia* (section *Ophiocaulon*).

(ii) WOOD

Vessels extremely small to large, few to numerous, sometimes in radial multiples of 4 or more cells or with a radial or oblique pattern, perforations usually simple, rarely with a few scalariform plates, intervacular pitting alternate, minute to moderately large, with horizontal apertures, pits to

parenchyma similar or larger and almost simple; members usually of medium length to moderately long, but extremely long in *Soyauxia*; 'fibriform vessel members' characteristic of some genera. **Parenchyma** typically apotracheal, diffuse to numerous uniseriate bands, occasionally with broader bands, aliform or vasicentric. **Rays** up to 1-8 cells wide, high, usually composed entirely of square or upright cells, but normally heterogeneous in a few species. **Fibres** with simple or distinctly bordered pits, moderately to very long.

Soyauxia differs considerably from the other genera, particularly in having solitary vessels, scalariform perforation plates, scalariform to opposite intervascular pitting, less abundant and diffuse parenchyma, and a different type of ray.

LEAF

Usually dorsiventral, but isobilateral in species of *Adenia*, *Paropsia*, *Passiflora*, *Tryphostemma*. **Hairs** unicellular or uniseriate in various species of *Passiflora*, the unicellular ones hooked at the apex in certain species. Uniseriate hairs also recorded in *Paropsia* and *Tacsonia*, those of the last genus sometimes very long or sufficiently interwoven to form a felt. Simple, unicellular, sclerenchymatous, and tufted trichomes recorded in *Abatia*, the tufted ones in *A. verbascifolia* H. B. et K. said to be formed by the union at their bases of a number of unicellular hairs. Glandular shaggy hairs (Fig. 152 D), each usually with a spherical head on a multiseriate stalk of variable length, the latter sometimes containing a vascular bundle, occur in a number of species of *Passiflora*, especially in the section *Dysomia*. Sessile or short-stalked glands recorded on the petioles of *Adenia*, *Crossostemma*, *Deidamia*, *Hollrungia*, *Paschanthus*, *Passiflora*, *Smeathmannia*, *Tacsonia*, *Tetrastylis* and glandular spots on the lower side in a few species of *Adenia*, as well as in *Passiflora*, particularly in the sections *Cieca*, *Decaloba*, *Murucuja*, *Pseudomurucuja*, *Psilanthus*. **Cuticle** of *Abatia* said to exhibit markings like those on etched glass. Cuticular projections to the epidermis common in species of *Passiflora*, especially in the sections *Cieca*, *Decaloba*, *Eumurucuja* (this applies to the stem also). **Epidermis** partly or wholly 2-layered, often with crystals in the lower layer, in a few species of *Abatia*, *Adenia*, *Hollrungia*, *Smeathmannia*; cells sometimes with mucilaginous inner membranes in *Barteria* and *Paropsia*. Lower epidermis frequently papillose in *Adenia* and *Passiflora*. **Hypoderm** recorded in a few species of *Abatia*. **Stomata** usually confined to the lower surface; mostly ranunculaceous, but a proportion said to be rubiaceous in *Abatia*. Central part of the **mesophyll** stated to contain thick, pitted cells in 1 species of *Mitostemma* and sclerenchymatous idioblasts in a few species of *Passiflora*. Vascular bundles of the **veins** usually embedded in the mesophyll; not always accompanied by sclerenchyma. **Petiole** examined only in 1 species of *Passiflora* (Fig. 154 D), in which transverse sections through the distal end exhibit a circle of individually distinct vascular bundles accompanied by smaller strands in the wings. **Secretory elements** include frequent cells and receptacles with tanniniferous contents, the receptacles recorded particularly in species of *Adenia* belonging to the section *Ophiocaulon*, where they sometimes appear as black dots. **Crystals** solitary or clustered; large solitary types said to occur in special sacs in certain species of *Adenia* (Fig. 152 C) and *Soyauxia* (in the mesophyll).

Axis

STEM (Fig. 154 H)

Young stems sometimes winged, e.g. in species of *Adenia* and *Passiflora*.

Epidermis encrusted with a wax-like substance on young shoots of several

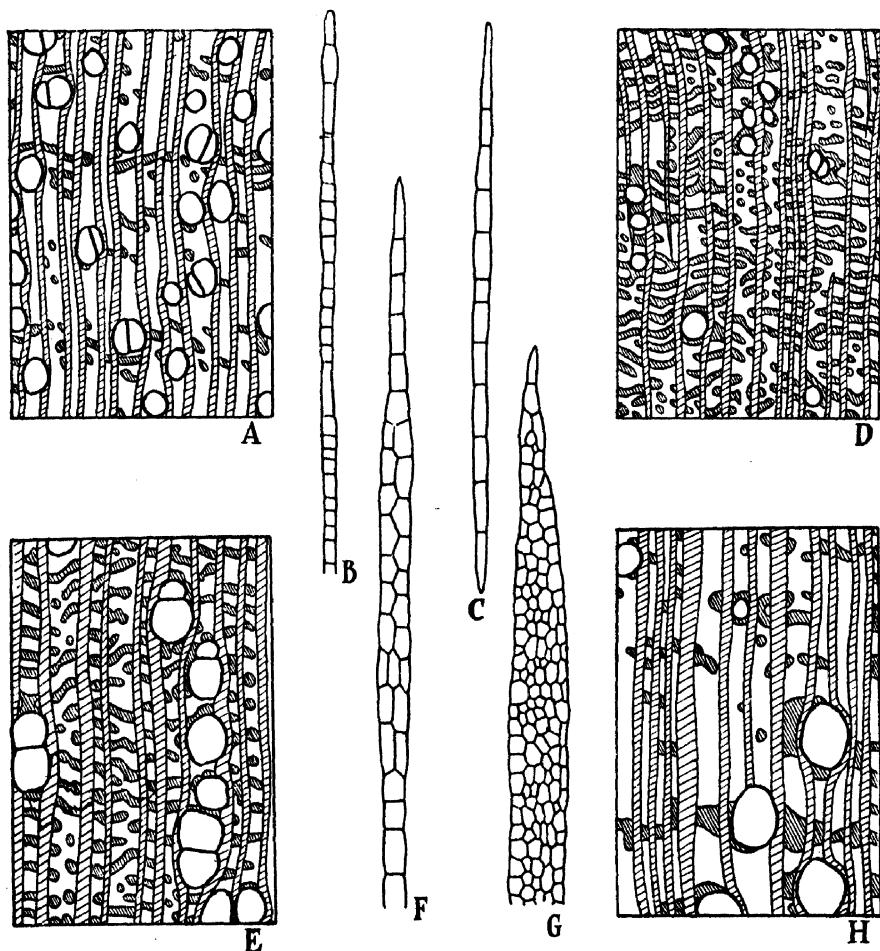


FIG. 153. PASSIFLORACEAE

A, *Soyauxia grandifolia* Gilg et Stapf. B, *S. grandifolia* Gilg et Stapf. C, *Androsiphonia adenostegia* Stapf. D, *A. adenostegia* Stapf. E, *Smeathmannia pubescens* Sol. F, *S. pubescens* Sol. G, *Crosso-stemma laurifolium* Planch. H, *Dilkea johannesii* Rodr.

species of *Adenia*. Warty excrescences arising in the hypoderm recorded by Baccarini (60) on old stems of *Adenia venenata* Forsk. (syn. *Modecca abyssinica* Hochst.). **Cork** arising superficially, sometimes in the epidermis itself; usually composed of thin-walled cells; spongy cork consisting of radially elongated cells present in *Passiflora suberosa* Linn. **Pericycle** commonly containing widely spaced strands of fibres, e.g. in species of *Passiflora* (Fig. 154 H); but provided with a composite and continuous ring of scleren-

chyma in *Mitostemma glaziovii* Mast. and relatively old branches of species of *Barteria*, *Paropsia*, *Paropsiopsis*, *Smeathmannia*, *Soyauxia*. Walls of the pericyclic fibres of certain species of *Passiflora* said to be stained violet, and the middle lamella yellowish, when treated with chlor-zinc-iodide. **Phloem** seen to include small groups of fibres in a species of *Passiflora*. **Xylem** in the form of a more or less continuous cylinder, but frequently traversed by broad primary rays; that of the climbing species includes a proportion of vessels of wide diameter (Fig. 154 H). Vessel perforation mostly simple, but, according to Harms (894), scalariform plates are common in *Barteria*, *Paropsia*, *Paropsiopsis*, *Smeathmannia* (see also 'Wood'). **Secretory elements** include tannin sacs with wide lumina, often with thick walls and sometimes vertically elongated, in the cortex and/or pith of a few species of *Adenia*, *Holrurgia*, *Passiflora*. **Crystals** include solitary and clustered types.

Bailey (70) has pointed out that in an unswollen branch of *Barteria fistulosa* Mast. the homogeneous pith consists of compact, thin-walled parenchyma. When part of the stem of this species develops into an **ant domatium**, the pith becomes heterogeneous and the reduced vascular system consists of separate bundles. The cavity of the domatium is surrounded by a few thin-walled cells containing an amber-coloured substance. The structure of the ant domatia of *B. dewerei* v. Willd. et Dur. is similar.

Some of the climbing members of the family, e.g. species of *Passiflora* and *Tetraphaëa*, possess **tendrils** believed to be morphologically equivalent to inflorescence branches. The anatomical structure of these becomes modified by the combined stimulus of contact and tension, whereby the development of mechanical tissue is increased, particularly in those parts of the tendril where it is most effective. Experiments have shown that the tendrils in *Passiflora* do, in fact, possess a greater breaking strength in consequence of these anatomical changes. Contact is said to be the main influence which causes an increase in the number of xylem elements and in the thickness of their walls, whereas tension causes the walls of the pith cells to become much thicker. For details of tendril structure see Brush (298), Bird (199), Gangstad (741). Stems of the succulent *Adenia venenata* Forsk. (syn. *Modecca abyssinica* Hochst.) include abundant water-storage parenchyma formed, according to Baccarini (60), partly by subdivision of the ground parenchyma, and partly by cambial activity. The intervacular parenchyma becomes lignified in old stems.

WOOD (Fig. 153)

Vessels very variable in size even in different species of the same genus, small (less than 100 μ mean tangential diameter) in at least some species of *Androsiphonia*, *Paropsia*, *Passiflora*, and *Soyauxia*, medium-sized (100–200 μ) in some species of *Crossostemma*, *Dilkea*, *Smeathmannia*, and *Tacsonia*; mean tangential diameter often more than 200 μ in climbing species, e.g. *Passiflora quadrangularis* L., and with individual vessels up to 400–500 μ , e.g. in *P. vitifolia* H. B. et K. (2466); solitary in *Soyauxia*, solitary and in pairs and threes in the other genera, with multiples or groups of 4 or more cells in *Androsiphonia*, *Paropsia* p.p., *Passiflora* p.p., and *Smeathmannia*; forming a radial pattern in *Smeathmannia* (Fig. 153 E) and in radial or oblique lines in *Passiflora* p.p., e.g. *P. gigantifolia* Harms and *P. emarginata* H. B. et K.; tending

to be grouped tangentially in *Tacsonia*. Variable in number even within a genus, e.g. 2.5 per sq. mm. in *Paropsia vareciformis* Mast. and 26 per mm. in *P. schliebenii* Sleumer, less than 5 per mm. also in *Passiflora* p.p. and 20 or more per mm. in *Crossostemma* and *Soyauxia*; tending to be ring-porous in *Passiflora* p.p. (1851) and in *Paropsia schliebenii*. Perforations usually simple only, but with a few scalariform plates in *Androsiphonia* and *Mitostemma glaziovii* Mast. (2158);¹ perforation plates exclusively scalariform in *Soyauxia*. Intervascular pitting typically alternate, minute, e.g. in some species of *Paropsia* and *Smeathmannia*, to moderately large, e.g. in *Dilkea*, usually with very distinct and sometimes exserted horizontal apertures that may coalesce, e.g. in *Crossostemma* and *Smeathmannia*; scalariform to opposite in *Soyauxia*; pits to wood and ray parenchyma usually similar to the intervascular pitting but sometimes larger, rounded or oblong, or nearly simple in some species of *Dilkea*, *Mitostemma* (2158), *Passiflora*, and *Tacsonia*, and scalariform in *Passiflora gigantifolia* and *Soyauxia*. Contents rare, tyloses observed in occasional specimens of *Dilkea* and *Passiflora*. Mean member length usually 0.5–1.0 mm., but up to 2.0 mm. in *Soyauxia grandifolia* Gilg et Stapf. Woodworth (2465, 2466) has recorded the occurrence of an unusual type of cell, which he terms a 'fibriform vessel member', in several species (all that were examined) of *Passiflora* and in *Smeathmannia pubescens* Soland. and *Tacsonia mollissima* H. B. et K.; these cells are similar in length, shape, &c., to the fibre-tracheids, being twice as long as the fusiform cambial initials, but have simple perforations. Similar cells were observed by the author in *Paropsia vareciformis* Mast., but none were observed in *Androsiphonia* or *Soyauxia*. Chalk and Chattaway (358) note the occurrence of perforated ray cells in *Androsiphonia*. **Parenchyma** moderately to very abundant, most typically apotracheal, as scattered cells and numerous uniseriate bands (Fig. 153 D and E); the bands very irregular and up to 4 cells wide in *Paropsia vareciformis*; less abundant and mainly as scattered cells in *Soyauxia* (Fig. 153 A); intermediate between broad metatracheal bands and aliform in *Dilkea* (Fig. 153 H); vasicentric only in *Crossostemma*. Crystals present in the ordinary cells in *Paropsia* and in chambered cells in *Tacsonia*. Strands often of more than 8 cells. **Rays** exclusively uniseriate in *Soyauxia* and almost so in *Androsiphonia*, up to 2–3 cells wide in *Paropsia*, *Passiflora* p.p., and *Smeathmannia*, up to 5–8 cells in some species of *Adenia* (2158), *Crossostemma*, *Dilkea*, *Keremanthus* (2158), *Passiflora* (2158), and *Tacsonia*, fewer and with some procumbent cells in *Crossostemma*; multiseriate rays typically high, less than 1 mm. only in *Tacsonia*; uniseriate rays usually numerous, and composed entirely of square to upright cells; often high; 8–18 rays per mm., least numerous (8–10 per mm.) in *Crossostemma* and *Tacsonia* and most numerous (15–18 per mm.) in *Androsiphonia*, *Dilkea*, and *Passiflora* p.p.; usually composed almost entirely of square or upright cells, with square cells in the centre, except in *Soyauxia* (Fig. 153 B), in which rows of square cells alternate with upright cells (Kribs's Type Heterogeneous III); the central, multi-seriate parts in *Crossostemma laurifolia* Planch., *Paropsia vareciformis*, and *Tacsonia mollissima* H. B. et K. consist of procumbent cells, with uniseriate margins of square or upright cells, the uniseriate margins commonly of 10 or

¹ Harms (894) refers to the abundant occurrence of scalariform perforation plates in *Barteria*, *Paropsia*, *Paropsiopsis*, and *Smeathmannia*.

more cells, except in *Tacsonia*; consisting mainly of procumbent cells in *Crossostemma*. In woods with few or no procumbent cells, particularly *Androsiphonia*, *Passiflora* p.p., and *Smeathmannia*, the cells, as seen in cross-section, are barely distinguishable in size and shape from the wood parenchyma cells, and Solereder notes that in *Tryphostemma littorale* Engl., and some species of *Adenia*, the cells are often elongated more in the tangential than in the radial direction. Crystals observed in the ordinary cells of *Crossostemma*, *Dilkea*, *Paropsia*, *Smeathmannia*, and *Tacsonia*, often abundant. **Fibres** with bordered pits, which are often large and distinct in *Crossostemma*, *Dilkea*, *Smeathmannia*, *Soyauxia*, and *Tacsonia*, and also, according to Solereder, in some species of *Adenia*, *Hollrungia*, *Passiflora*, and *Tryphostemma*; with simple pits in some species of *Androsiphonia*, *Paropsia*, and *Passiflora* and, according to Solereder, of *Adenia* and *Keramanthus*; walls moderately to very thick, the latter particularly in the species with simple pits. Mean length 1.9–2.9 mm., longest in *Soyauxia*. Woodworth (2465) notes some libriform fibres in *Passiflora* spp., a preponderance of libriform fibres, with very few fibre-tracheids, in *Smeathmannia pubescens* Sol., and only a few fibre-tracheids in *Androsiphonia*. Woodworth (2466) also refers to short septate fibre-tracheids in *Passiflora vitifolia* H. B. et K.

TAXONOMIC NOTES

(i) FROM GENERAL ANATOMY

This family appears to have points in common with the Flacourtiaceae. It is, in fact, difficult to decide to which of the 2 families some of the genera belong. Harms (894) has pointed out that *Barteria*, *Paropsia*, *Paropsiopsis*, and *Smeathmannia* differ from most members of the family in having frequent scalariform perforation plates to the vessels, as well as in the presence of sclerenchymatous elements between the primary groups of fibres in the pericycle.

(ii) FROM WOOD STRUCTURE

Soyauxia has been included here, following Hutchinson. In some respects it appears to have more in common with the Flacourtiaceae, cf. *Idesia*; on the other hand, it might be fitted into the Passifloraceae on the assumption that it is a primitive type, of which there is ample evidence in the wood structure. No 'fibriform vessel members' have been observed in *Soyauxia*, but its ordinary vessel members are extremely long and rather narrow and are actually longer than the 'fibriform vessel members' measured by Woodworth (2466).

Smeathmannia has been included here rather than in the Flacourtiaceae and kept separate from *Paropsia*, though the woods of the 2 genera are very similar. The occurrence of 'fibriform vessel members' in both genera supports their affinity with *Passiflora* and *Tacsonia*, though there are many very obvious differences between them; some of the latter may perhaps be related to differences in habit.

Tacsonia has been kept separate from *Passiflora*. Woodworth (2466) found macerated material of *Tacsonia mollissima* H. B. et K. to be strikingly similar to that of *Passiflora* spp. On the other hand, in the limited material available to the author, the 2 genera appeared to be distinct.

ECONOMIC USES

Species of *Passiflora*, known as Passion Flowers, are cultivated in Great Britain under glass or in sheltered places out of doors. The fruits of certain species of *Passiflora* are commonly eaten in tropical countries, especially America and the West Indies. The best-known edible species are Grenadillas (*P. quadrangularis* Linn. and *P. macrocarpa* Mast.), Belle Apple (*P. laurifolia* Linn.), Sweet Cup or Pomme d'Or (*P. maliformis* Linn.).

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Abatia, Adenia, Barteria, Crossostemma, Deidamia, Hollrungia, Mitostemma, Paropsia, Paropsiopsis, Paschanthus, Passiflora,* Smeathmannia, Soyauxia, Tacsonia, Tetrastylis,* Tryphostemma.

* Represented in the Kew Slide Collection.

(ii) FOR WOOD STRUCTURE

(Adenia), Androsiphonia, Crossostemma, Dilkea, (Hollrungia), (Keramanthus), (Mitostemma), Paropsia, Passiflora, Smeathmannia, Soyauxia, Tacsonia.

LITERATURE

(i) On General Anatomy

Baccarini 60, Bailey 70, Bird 199, Bohmker 216, Brush 298, Gangstad 741, Harms 894.

(ii) On Wood Structure

Burgerstein 310, Chalk and Chattaway 358, Cooper and Record 461, Cozzo 494, Harms 894, Record 1843, 1851, Woodworth 2465, 2466.

148. ACHARIACEAE

SUMMARY

A small South African family, consisting of the low half-shrub *Acharia tragioides* Thunb., and the climbers *Ceratiosicyos ecklonii* Nees and *Guthriea capensis* Bolus, the last species being a stemless herb with fleshy roots arising from a rhizome. The anatomy has not been very fully investigated, and the following account has been taken from Harms (895) and Solereder.

LEAF

Dorsiventral in *Acharia* and *Ceratiosicyos*, with about 1 layer of palisade tissue. **Hairs** in *Acharia* simple, multicellular, with fairly thick walls. **Stomata** in *Acharia* and *Ceratiosicyos* confined to the lower surface. Vascular bundles of the **veins** not accompanied by sclerenchyma in either genus.

AXIS

STEM

Young stem angular in *Acharia*, but a few layers of **cork** subsequently arise on the inside of the collenchyma in the angles, and in the sub-epidermis between the angles. **Pericycle** in *Acharia* and *Ceratiosicyos* containing isolated strands of fibres. **Xylem** generally including vessels with simple perforations, but scalariform plates with a few bars recorded locally in *Acharia*, especially

in the region of the primary xylem. Vessels of *Acharia* narrow, radially arranged, with bordered pits, embedded in a ground-mass of thick-walled, septate fibres with simple pits. Vessels of *Ceratosicyos* mostly wide and scattered, embedded in ground-tissue consisting of occasionally septate, prosenchymatous, simple-pitted elements intermixed with parenchyma, the latter being mostly situated around the vessels. Rays broad in *Ceratosicyos*.

TAXONOMIC NOTES

The genera in this family were included under Passifloraceae in the Bentham and Hooker system, but they were placed in a separate family by Harms (895) owing to differences in floral structure.

GENERA DESCRIBED

Acharia, *Ceratosicyos*.

LITERATURE

On General Anatomy
Harms 895.

149. CARICACEAE

(FIG. 154 on p. 682)

SUMMARY

This tropical American family consists of the genera *Carica*, *Cylicomorpha*, *Mocinna*, and *Jacaratia*, members of which are shrubs or small trees with somewhat fleshy trunks bearing terminal clusters of leaves. The Pawpaw (*Carica papaya* Linn.) has received more attention from anatomists than any of the other members of the family, and the following description refers to this species. Chatterji (378) has described the anatomical changes which occur in *Carica papaya* when affected by a physiological disease. See under 'Axis' on p. 683.

LEAF

Dorsiventral, with well-developed intercellular spaces in the spongy tissue. Long, club-shaped, glandular **hairs** with multicellular heads present on the petiole and along the principal veins. **Stomata** confined to the lower surface; ranunculaceous. **Petiole** (Fig. 154 A), in transverse sections through the distal end, exhibiting a circle of numerous widely spaced collateral vascular bundles surrounding a very large, parenchymatous pith. Other strands, consisting wholly of phloem, also occur in the vascular ring interspersed between the collateral bundles. Articulated **laticiferous canals** accompany the vascular bundles of the veins and extend into the surrounding mesophyll. All parenchymatous tissues stated to contain refractive grains of a substance in the nature of an aldehyde. Clustered **crystals** of calcium oxalate fairly abundant.

AXIS

STEM (Fig. 154 E)

Glandular **hairs**, similar to those described for the leaf, present on the young internodes of the stem. Stem swollen at the base owing to dilation of

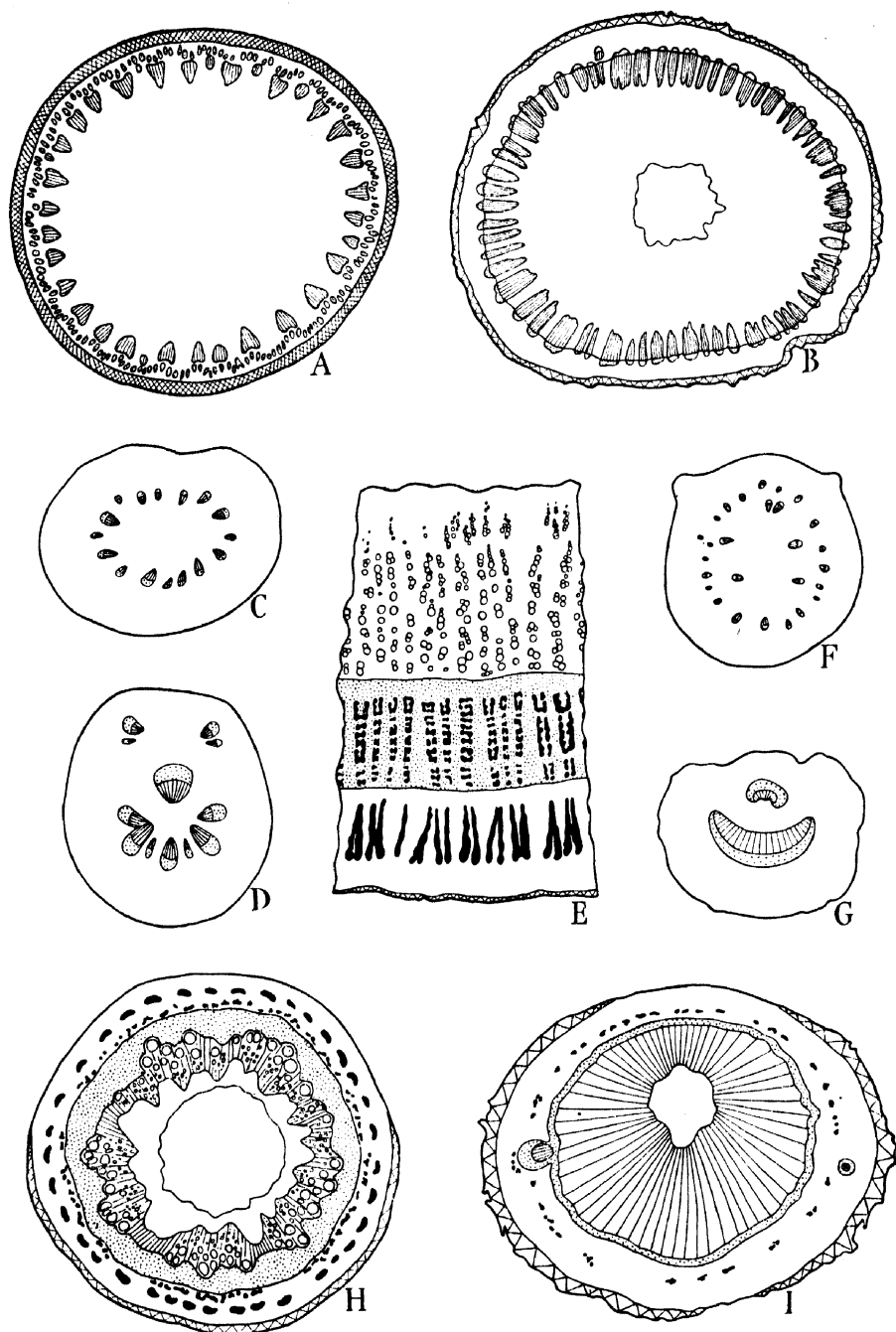


FIG. 154. *CARICACEAE*, A and E; *BEGONIACEAE*, B-C and F; *PASSIFLORACEAE*, D and H; *TURNERACEAE*, G and I

A, *Carica papaya* Linn. Petiole $\times 5$. B, *Begonia manicata* Cels. Stem $\times 5$. C, *B. echinosepala* Regl. Petiole $\times 7$. D, *Passiflora racemosa* Brot. Petiole $\times 13$. E, *Carica papaya* Linn. Stem $\times 5$. F, *Begonia manicata* Cels. Petiole $\times 6$. G, *Turnera ulmifolia* Linn. Petiole $\times 18$. H, *Passiflora racemosa* Brot. Stem $\times 13$. I, *Turnera ulmifolia* Linn. Stem $\times 18$.

the primary cortex and pith. Primary **cortex** largely composed of collenchyma. **Pericycle** including massive, isolated strands of fibres, in the form of caps to the well-developed, radially elongated groups of phloem. Secondary **phloem** stratified into hard and soft portions. Conducting system consisting of a circle of narrow, radially elongated **vascular bundles**, separated from one another by broad, parenchymatous rays. Ground tissue of the **xylem** composed of wedges of unligified, parenchymatous tissue. Vessels mostly about 200 μ in radial diameter, solitary, or, more frequently, in approximately radial multiples of up to 5 or occasionally more members. Lateral walls of the vessels with reticulate thickening and large, simple, gash-like pits where in contact with the parenchyma, and almost circular intervacular pitting. Perforations simple and horizontal. Wood fibres absent. A network of articulated **laticiferous canals**, with contents which are stained yellow by iodine, present in all parts of the ground tissue. Clustered **crystals** abundant in the cortex.

Chatterji (378) has described an apparently physiological disease of *Carica papaya* in which the leaves at first assume an unhealthy green colour, whilst the margins become curled. Dark-green blisters also arise on the lamina. Later on the lamina becomes dissected until, in extreme cases, only the mid-rib remains. The leaves eventually turn brown and fall off, whilst the whole plant becomes stunted. Degeneration begins in the laticiferous system, but later the elements of the secondary phloem are affected. Hypertrophy eventually sets in, not only amongst the laticiferous elements and phloem, but also in the mesophyll.

ECONOMIC USES

The large, edible fruits of *Carica papaya* Linn. are much relished in tropical countries, where the Pawpaw is widely cultivated. Papain, a drug with digestive properties, is obtained from the latex from the unripe fruits.

GENUS DESCRIBED

Carica.*

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Chatterji 378, Harms 896, Stephens 2194.

(ii) *On Wood Structure*

Howard 1088, Record 1783, 1843, 1851, Record and Hess 1886, Rowlee 1964, Williams 2430.

150. MALESHERBIACEAE

SUMMARY

Malesherbia consists of erect or procumbent herbs or half-shrubs which occur in dry habitats in the Andes from Peru to Bolivia and in the Argentine. The following account of the anatomy is taken largely from Harms (893).

LEAF

Isobilateral. **Hairs** of 2 types. (i) Moderately stiff unicellular trichomes.

(ii) Long, filiform, multiseriate, frequently glandular hairs, secreting a substance with an unpleasant smell.

AXIS

STEM

Cork arising in the epidermis, sub-epidermis, or cortex in different species; consisting of thin-walled cells. **Cortex** said to include many layers of palisade cells in *M. fasciculata* Don. **Pericycle** containing isolated strands of fibres. **Xylem** including numerous, radially arranged vessels, mostly with simple, circular or elliptical perforations, but scalariform plates with a few bars recorded in the neighbourhood of the primary wood. Wood fibres consisting of fairly short elements with very small, slit-shaped or elliptical pits. Rays mostly 1-2, rarely 3, cells wide.

GENUS DESCRIBED

Malesherbia.

LITERATURE

On General Anatomy
Harms 893.

151. CUCURBITACEAE

(FIG. 155 on p. 686; FIG. 156 on p. 686; FIG. 157 on p. 688)

SUMMARY

Mostly herbs, often scandent or prostrate, but some species tending to be woody. The family is noted for its rapid vegetative growth. Most members of the family are tropical. Many species are provided with **tendrils** of which those in *Cucumis* have been interpreted, according to Trinkgeld (2279), as metamorphosed leaves, whilst those in other genera are homologous with stems bearing leaves. Tendrils become coiled round cylindrical supports with which they come into contact, but form anchoring pads when in contact with flat surfaces. Debberman (553) has shown that in *Gymnopetalum* contact between the anchoring pad and its supporting surface is maintained by hair-like papillae which grow out from the pads and fit very exactly into crevices and depressions in the surface. Debberman concluded, from less detailed observations on other species, that this mode of attachment is general throughout the family. Glandular **hairs** with multiseriate stalks are very characteristic, but simple unicellular or uniseriate types as well as wart-like or spiny trichomes also occur. Calcareous **cystoliths** and similar bodies occur, usually at the bases of the hairs or in adjacent epidermal cells, more rarely in epidermal cells away from the trichomes. They vary considerably in size and shape in leaves of an individual species at different stages of development. **Extra-floral nectaries** and glandular leaf-teeth are fairly frequent. The **stomata**, which occur on both sides of the leaf or are confined to the lower surface, are ranunculaceous. They are frequently raised above the general level of the epidermis, especially in stems. The **petiole**, in transverse sections through the distal end, exhibits a crescent or circle of vascular bundles of which the

larger ones are bicollateral. In the **axis** the most noteworthy feature is the predominantly bicollateral **vascular bundles**, separated from one another by broad strips of ground tissue, and frequently arranged in 2 rings. Their course in the axis has been described by Zimmerman (2508), Manteuffel (1435), and other authors. The **xylem** in the old stems sometimes becomes cleft through the development of secondary medullary rays. The **sieve tubes**, which are usually large and conspicuous, occur scattered in the cortex as well as in the phloem in a number of genera. There is a closed **ring of sclerenchyma** in the outer part of the cortex of herbaceous species, and a continuous ring of fibrous cells in the **pericycle** of young stems, but this may become discontinuous when older. **Anomalous structure** is fairly frequent in thick stems and roots.

LEAF

Usually dorsiventral, more rarely isobilateral. **Hairs** include the following types. (i) Simple, unicellular or uniseriate, sometimes accompanied by subsidiary cells at the base. (ii) Wart-like or spiny trichomes in species of *Bryonia*, *Cucumis*, *Cucurbita*, *Ecballium*. (iii) Glandular hairs with uniseriate stalks of variable length and spherical or disk-shaped heads in species of *Abobra*, *Benincasa*, *Citrullus*, *Corallocarpus*, *Cucumis*, *Cucurbita*, *Cyclanthera*, *Ecballium*, *Fevillea*, *Gynostemma*, *Kedrostis*, *Lagenaria*, *Luffa*, *Melothria*, *Momordica*, *Trichosanthes*, *Zanonia*. (iv) Explosive hairs with uniseriate stalks of 5 or 6 cells and 2-celled heads in *Curcubita* and *Momordica*. According to Zimmerman (2508) the whole head of each hair is explosively cast off and the contents extruded through the pore thus formed. (v) Water-containing hairs, chiefly situated at the leaf margins; those of *Momordica* spp. multicellular, elongated; with pointed apices in species of *Bryonopsis*, *Coccinia*, *Melothria*, *Raphanistocarpus*. (vi) A network of uniseriate hairs, covered with waxy material, recorded in *Telfairia*. (vii) Hooked, calcified hairs in *Peponium*. (Types iv to vii recorded by Zimmerman, 2508.) **Leaf-teeth** sometimes secretory, e.g. in *Cucumis*. **Extra-floral nectaries**, occurring all over the lower surface or confined to the bases of the leaves, recorded in species of *Abobra*, *Adenopus*, *Alsomitra*, *Bryonia*, *Cephalandra*, *Cucurbita*, *Fevillea*, *Lagenaria*, *Luffa*, *Momordica*, *Sphaerosicyos*, *Trichosanthes*. Large, black glands (1 opposite pair near the distal end of the petiole, and others on the lower surface of the lamina near the vein endings) noted at Kew in *Sphaerosicyos sphaericus* (E. Mey.) Hook. f. The material secreted appeared to be mucilaginous. Cells of the **epidermis** particularly large in Japanese species of *Actinostemma*, *Benincasa*, *Citrullus*, *Cucumis*, *Cucurbita*, *Gynostemma*, *Melothria*, *Momordica*, *Schizopepon*.

Stomata confined to the lower side or present on both surfaces; ranunculaceous; frequently raised on papillose projections above the general level of the epidermis in the same way as in the stem (see p. 687), although in fewer species. **Mesophyll** containing silicified cells in *Fevillea* and *Zanonia*. **Midrib** reported by Solereder to be provided with: (i) A single vascular bundle in species of *Actinostemma* and *Schizopepon*. (ii) A large strand accompanied by a smaller one in *Melothria* sp. (iii) A large bundle and 2 small lateral ones in *Gynostemma* sp. (iv) A large bundle with 2 smaller ones above it in species of *Benincasa*, *Cucumis*, *Lagenaria*. (v) Four bundles arranged in the form of a

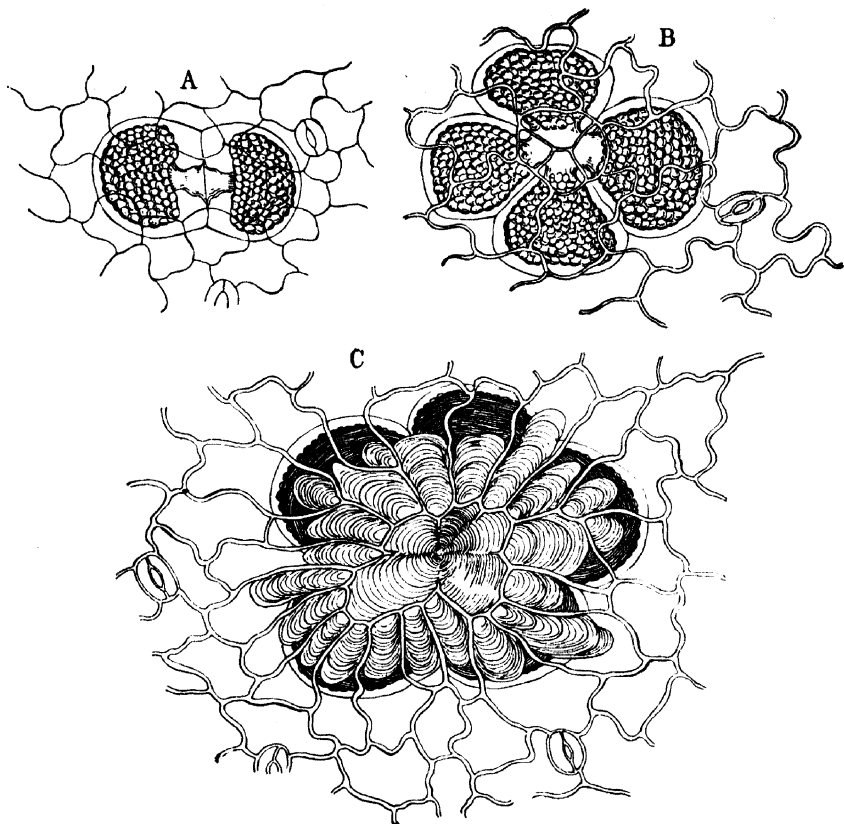


FIG. 155. CUCURBITACEAE

Double cystoliths and groups of cystoliths in *Momordica*: A, B, *Momordica* sp.; C, *Momordica charantia* L.—After Penzig.

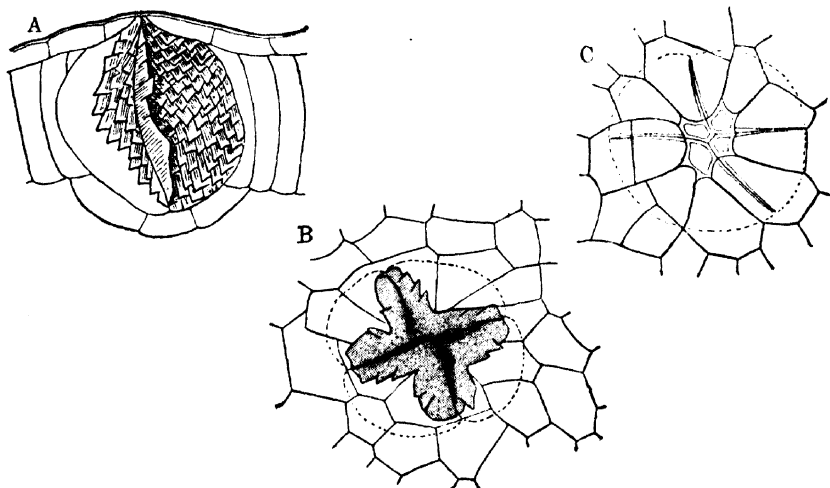


FIG. 156. CUCURBITACEAE

Deposits of calcium carbonate in the leaf of *Hanburia mexicana* Seem. A, Incrusted group of cells in a transverse section of the leaf; B, in surface-view (before decalcification; the central epidermal cells lying above the cell-group are not figured); C, in surface-view after decalcification.—By Solereder.

cross in *Luffa*, *Momordica*, *Trichosanthes*. (vi) A ring of bundles in species of *Citrullus* and *Cucurbita*. **Petiole**, in transverse sections through the distal end, exhibiting an almost closed crescent or circle of bundles, the larger ones bicollateral, in *Bryonia* (Fig. 157 D), *Cucumis*, *Cucurbita*, *Cyclanthera* (pro parte), *Ecballium*, *Lagenaria*, *Luffa*, *Melothria*, *Sicyos*. Bundles likewise separate but arranged in a slightly more open crescent in species of *Alsomitra* (Fig. 157 F), *Cyclanthera* (pro parte) (Fig. 157 B), as well as in *Echinocystis*. Chakravarty (348) has also drawn attention to the constancy in the number and structure of the vascular bundles in the midribs and petioles of cucurbitaceous leaves, which he believes to be of generic diagnostic value.

Cystoliths (Figs. 155 A-C and 156 A-C), varying widely in size and shape and frequently visible to the naked eye as white areas, commonly occur at the bases of hairs and in neighbouring epidermal cells of numerous genera and species. Less frequent in epidermal and adjacent mesophyll cells not immediately associated with the hairs. The form and size of cystoliths vary considerably within a species at different stages in the development of the leaves; those in species of *Adenopus*, *Cucumis*, *Cyclantheropsis*, *Gerrardanthus*, *Melothria* described by Zimmerman (2508) as becoming disorganized and disappearing from the leaves when sufficiently old. **Crystals** infrequent in or absent from many genera and species; recorded, chiefly as clusters, in a few species of *Gerrardanthus* and *Momordica* (Zimmerman 2508) and solitary and clustered crystals together with crystal-sand in the same genera (Chakravarty 348).

AXIS

STEM (Fig. 157 A, C, and E)

Frequently angular, with collenchyma in the ribs. **Stomata** raised above the general level of the epidermis, at the apices of small projections, in species of *Adenopus*, *Benincasa*, *Cucurbita*, *Luffa*, *Momordica*, *Peponium*, *Physedra*, *Sechium*, *Sphaerosicyos*. Stomata said by Zimmerman (2508) to be at the same level as or only slightly raised in species of *Coccinia*, *Cyclantheropsis*, *Gerrardanthus*, *Kedrostis*, *Melothria*, *Momordica*, *Raphanistrocarpus*, *Telfairia*, *Trochomeria*. **Cortex** often including a large proportion of collenchyma, especially in the ribs, but with the collenchyma sometimes interrupted by patches of assimilatory tissue extending to the epidermis. Outer part of the cortex, containing a sinuous ring of sclerenchyma, the latter being continuous in young stems, but becoming interrupted during secondary thickening, although the individual groups sometimes become more or less reunited by secondary sclerenchymatous cells. Cortex and medullary rays in old stems sometimes including groups of stone cells. **Cork** not observed in many species, but, when seen, arising at different levels, e.g. according to Zimmerman (2508) in the sub-epidermis in *Kedrostis* sp.; in the outer part of the cortex in *Cyclantheropsis* sp., on the inside of the sclerenchymatous ring in the cortex in *Melothria* sp. Solereder records it as arising in the cortex in *Zanonia indica* Linn. and near the outer periphery of the pericyclic sclerenchyma in *Trichosanthes*. **Pericycle** containing a continuous ring of fibrous cells in very young stems, but the ring becomes discontinuous when older. **Vascular bundles** widely separated by broad strips of ground tissue; nearly always bicollateral and frequently arranged in 2, more or less distinct, circles;

vascular bundles of the inner ring almost meeting at the centre of the stem in some species; approximately constant in number and arrangement in an individual species according to Ghosh (762) and Zimmerman (2508), provided attention is confined to material of comparable age. Pellisier (1684) has emphasized, however, that the number of bundles is greater in transverse

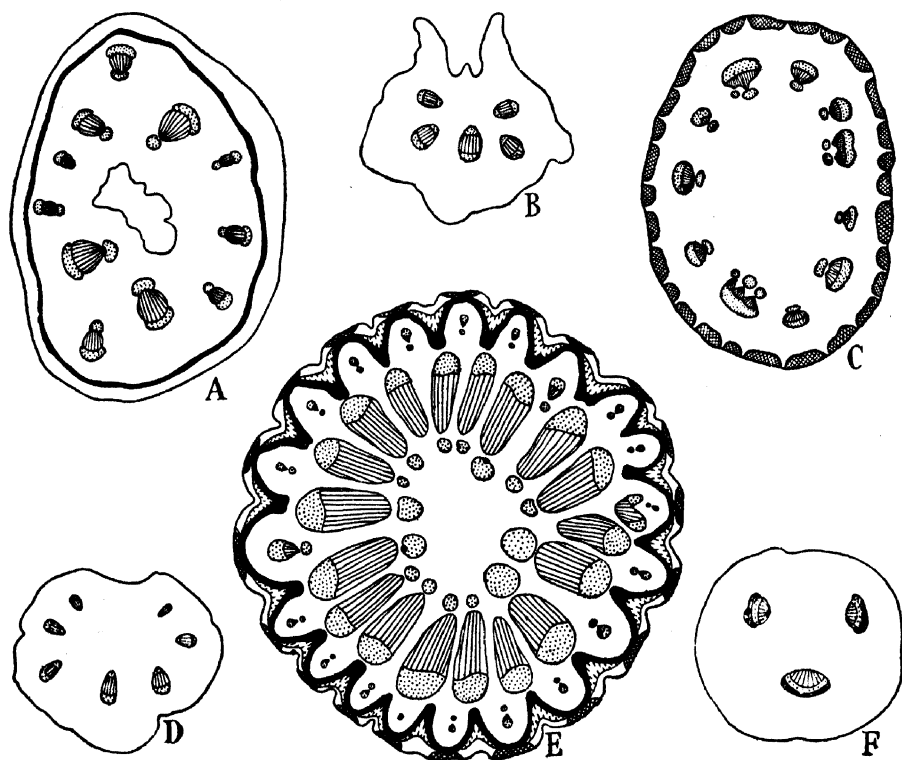


FIG. 157. CUCURBITACEAE

A, *Cucurbita* sp. Stem $\times 35$. B, *Cyclanthera explodes* Naud. Petiole $\times 55$. C, *Ecballium elaterium* A. Rich. Stem $\times 12$. D, *Bryonia dioica* Jacq. Petiole $\times 30$. E, *Acanthosicyos horrida* Welw. Stem $\times 18$. F, *Alsomitra sarcophylla* M. Roem. Petiole $\times 36$.

sections of old compared with young internodes of *Cucurbita*. Vascular bundles, situated outside the sclerenchymatous ring in the cortex, recorded by Zimmerman in a few species of *Actinostemma* and *Momordica*.

Zimmerman recognized the 3 following arrangements of vascular bundles in the young internodes. The differences are not constant throughout the genera mentioned. (i) Five bundles in the outer and 5 in the inner circle in *Adenopus*, *Blastania*, *Bryonopsis*, *Coccinia*, *Corallocarpus*, *Cucumis*, *Kedrostis*, *Luffa*, *Melothria*, *Momordica*, *Physedra*, *Raphanistrocarpus*, *Trochomeria*. (ii) Internode with less than 10 bundles in a few species of *Cucumis*, *Kedrostis*, *Melothria*, *Momordica*. (iii) Internode with more than 10 bundles, i.e. with 2 circles of 5 bundles each, accompanied by accessory, frequently reduced bundles in a few species of *Coccinia*, *Cucurbita*, *Gerrardanthus*, *Lagenaria*,

Peponium, *Sphaerosicyos*, *Telfairia*. Zimmerman also classified stems according to the arrangement of the sieve tube tissue.

Further particulars concerning the course of the vascular bundles in *Bryonia* have recently been recorded by Bouvrain (248, 249) and Fourcroy (700, 701).

Collateral strands, formed through loss of the inner phloem, are present amongst the bicollateral bundles in numerous genera and species. Bundles exclusively collateral in species of *Alsomitra*, *Anisosperma*, *Cyclantheropsis*, *Gerrardanthus*; bicollateral structure also stated by Solereder to be obscure in species of *Fevillea*, *Gynostemma*, *Zanonia*. **Sieve tubes** wide, with conspicuous transverse sieve plates; sometimes occurring in the cortex as well as in the phloem in certain genera, e.g. in species of *Cucumis*, *Cucurbita*, *Ecbalium*, *Lagenaria*, *Zanonia*; those of the cortex and phloem respectively being united to one another in at least some species. Xylem and phloem often become dissected by the formation of secondary rays produced by the fascicular cambium, and the xylem by large groups of unligified elements also derived from cambial cells. Complete collateral bundles sometimes develop in the secondary rays in species of *Cyclantheropsis* and *Gerrardanthus*. **Interxylary phloem** (see 'Anomalous Structure' on p. 690) sometimes arises in the unligified tissues of the xylem, e.g. according to Zimmerman in old stems of a few species of *Adenopus*, *Luffa*, *Melothria*, *Momordica*, *Physedra*, *Sphaerosicyos*. Interfascicular cambium in old stems of some genera also serves to enlarge the primary medullary rays with additional unligified tissue during secondary thickening, but, in some instances, phloem and xylem are also derived from it, e.g. according to Solereder in *Lagenaria*. **Xylem**, in very young stems, including narrow vessels, but those formed subsequently have conspicuously wide lumina, as is usual in rapidly growing scandent herbs and lianes; perforations simple. Tyloses common, especially in old stems; frequently becoming thick walled. **Giant nuclei**, up to $85\ \mu$ in diameter, recorded by Scott (2072) in the developing vessels of *Echinocystis macrocarpus* Britton, and others up to $66\ \mu$ in diameter in *Cucurbita pepo* L. **Pith** becoming hollow in many species, but persistent and ligified in others.

Bews (192) has described, in an undetermined species of *Benincasa*, how the central cavity of the pith becomes filled with a mass of tissue originating from a single cell which intrudes into the hollow centre of the stem. A secondary cavity arises within the intruding tissue, and becomes lined with thick-walled cells with abundant contents, while simple pluricellular and less frequent glandular hairs, resembling those on the outside of the stem, project into the secondary cavity from the surrounding cell layers.

Secretory elements apparently not recorded, and definitely absent from species in the Kew slide collection. **Cystoliths**, see p. 687. **Crystals** infrequent in or absent from most genera and species; clusters recorded by Zimmerman in the ground tissue, particularly of old stems, in species of *Gerrardanthus*, *Luffa*, *Momordica*, *Physedra*.

ROOT

Primary structure said by Holroyd (1081) to be tetrarch in 4 representative seedlings.

TUBEROUS ROOTS AND RHIZOMES

Tuberous roots and rhizomes exhibit a well-developed, amylofous, ground tissue, with weakly developed conducting elements embedded in it, according to Scott (2072) and Zimmerman (2508).

Root tubers of *Coccinia engleri* Gilg. described as follows by Zimmerman. Covered externally by a brown layer of cork. Ground tissue consisting of amylofous parenchyma, but cracks developing in it towards the centre of the root. Xylem, as seen in transverse sections, composed of isolated strands embedded in the ground tissue, most strands including a large solitary vessel. Small phloem strands present on the outside of the cambium ring, and others occur scattered in the ground tissue, particularly towards the inside of the xylem strands.

Stem tubers of '*Melothria argyrea*' somewhat similar in structure but xylem consisting of scattered strands arranged along certain radii, the phloem being situated chiefly along the same radii as the xylem.

ANOMALOUS STRUCTURE

The following anomalies have been recorded in roots. (i) Islands of soft interxylary phloem in species of *Cucurbita* and *Lagenaria*. (ii) Bundles of interxylary phloem, arising through the activity of interfascicular cambium, in the unligified tissue of the primary medullary rays of *Thladiantha dubia* Bge. and, according to Zimmerman (2508), complete vascular bundles in the corresponding position in *Momordica* sp. (iii) Concentric vascular bundles formed in the wood of *Bryonia dioica* Jacq. by the activity of cambial tissue surrounding individual groups of secondary vessels. (iv) Successive rings of growth arising in the pericycle of *Ecballium elaterium* A. Rich. (v) Thick roots of several members of the family provided with a pith containing groups of intraxylary phloem, the latter sometimes becoming converted to inversely orientated bundles. For formation of interxylary phloem and other anomalous tissues in stems see p. 689.

PHYLOGENETIC NOTES

Worsdell (2470), after studying the course of the vascular bundles in the Cucurbitaceae, both in stems and in 'conservative' parts of the axis such as the peduncle and node, drew conclusions concerning the phylogenetic origin of bicollateral bundles in general and of those of the Cucurbitaceae in particular. His chief views are as follows.

(i) 'The vascular system of the Cucurbitaceae represents the *vestige of a former ancestral scattered system* of bundles such as obtains in the Monocotyledons, of which only two series of rings remain in perfect condition, the rest appearing in the form of rudimentary external phloem strands (rarely bundles as well), "internal phloem" strands, and medullary bundles or phloem strands.' (ii) 'In the vegetative stem of certain members of the order (family), and, as a rule, in the *lower part* only, the internal phloem exists in the form of vascular bundles of which the xylem exists entirely or for the most part, on the *outer* side.' (iii) 'The "bicollateral" bundle of the Cucurbitaceae is a compound structure consisting of the more or less intimate association or attachment of two distinct vascular bundles, of which the innermost has lost the xylem.'

Chakravarty (348) has attempted to arrange some of the genera within the family in a phylogenetic sequence, assuming for this purpose that reduction in the number of vascular bundles is an advanced character.

ECONOMIC USES

The fruits of certain members of this family are the well-known gourds. Familiar gourds include Cucumbers (*Cucumis sativus* Linn.), Melons (*Cucumis melo* Linn.), Water-melons (*Citrullus vulgaris* Schrad.), Vegetable Marrows (*Cucurbita pepo* Linn.), whilst many others are familiar in tropical countries. Loofahs consist of the vascular system of the fruits of *Luffa cylindrica* Roem. and other species of *Luffa*. For particulars of the development of this vascular system see Sinnott and Bloch (2117). White Bryony or English Mandrake, at one time used to allay coughing in pleurisy, is the root of *Bryonia dioica* Jacq.

GENERA DESCRIBED

Abobra, Acanthosicyos,* Actinostemma, Adenopus, Alsomitra,†* Anisosperma, Benincasa, Blastania, Bryonia,* Bryonopsis, Cephalandra, Citrullus, Coccinia, Corallocarpus, Cucumis, Cucurbita,* Cyclanthera,* Cyclantheropsis, Ecballium,* Echinocystis,* Fevillea, Gerrardanthus, Gymnopetalum, Gynostemma, Hanburia, Kedrostis, Lagenaria, Luffa, Melothria, Momordica, Peponium, Physedra, Raphanistrocarpus, Schizopepon, Sechium, Sicyos,* Sphaerosicyos, Telfairia, Thladiantha, Trichosanthes, Trochomeria, Wilbrandia, Zanonina.

† Alsomitra Roem = Nealsomitra Hutch.

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Barkley 141, Bews 192, Bouvrain 248, 249, Chakravarty 348, Cogniaux 441, Crafts 496, Debberman 553, Fourcroy 700, 701, Ghosh 762, Hagerup 865, Holroyd 1081, Hutchinson 1116, Manteuffel 1435, Pellissier 1683, 1684, Sabnis 1977, Scott 2072, Balwant Singh 2513, Sinnott and Bloch 2117, Trinkgeld 2279, Werner 2414, Worsdell 2470, Zimmerman 2508.

152. BEGONIACEAE

(FIG. 154 on p. 682; FIG. 158 on p. 692; FIG. 159 on p. 692)

SUMMARY

A mainly tropical family consisting chiefly of herbs which are often succulent, but some species are shrubby or scandent, the xylem in the climbers often being excentrically developed. Some species possess rhizomes while others are stemless but provided with a basal tuber. The tissues have a well developed capacity for producing adventitious roots, and some of the ornamental begonias are cultivated from leaf cuttings. The **hairs** include various multicellular, non-capitate types as well as others with heads composed of a few or of many cells. The **stomata**, confined to the lower surface, are generally very characteristic in appearance owing to their being surrounded by 3-6 subsidiary cells often arranged in 2 rings. The stomata in some species are in

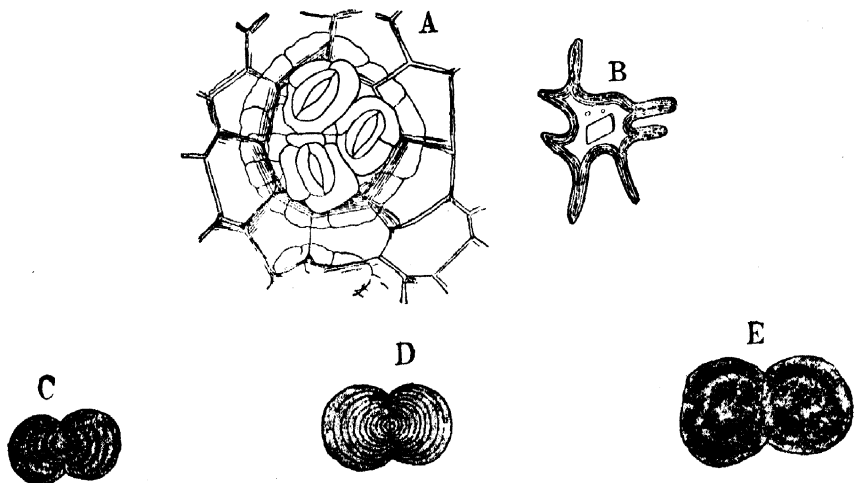


FIG. 158. *BEGONIACEAE*

A, Stomatal group of *Begonia fuchsiaeifolia* (A. DC.) Warb. B, Branched idioblast from the leaf of *Begonia arborescens* Raddi. C, Double cystotyle of *B. luxurians* Scheidw. D, Double cystotyle of *B. paleata* A. DC. after treatment with alcohol. E, Double cystosphere of *B. laetevirens* Van Houtte.—After Fellerer.

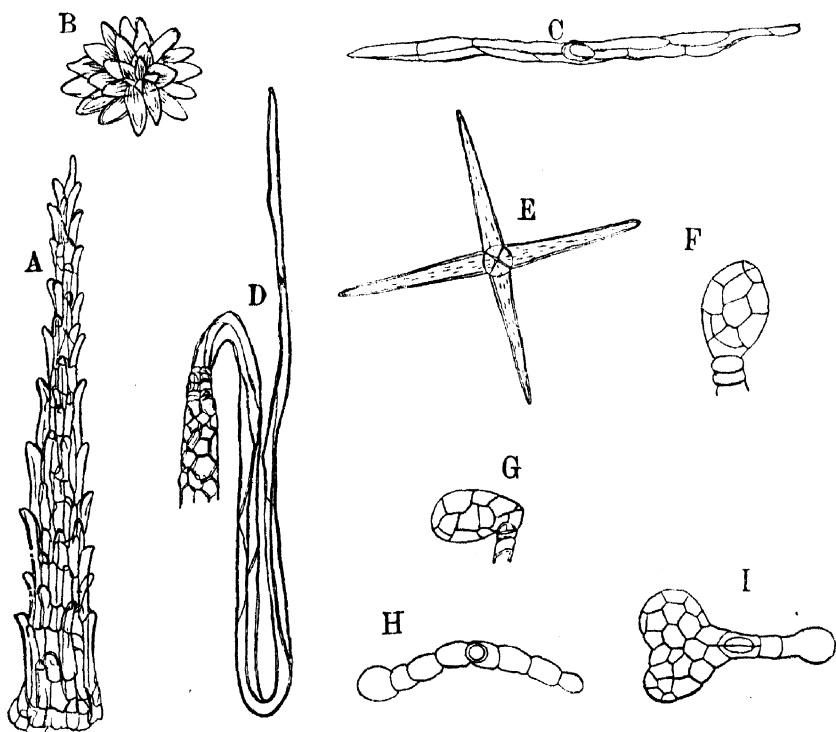


FIG. 159. *BEGONIACEAE*

Trichomes of: A, *Begonia hispida* Schott.; B, *B. parviflora* Poepp. et Endl.; C, *B. solananthera* A. DC.; D *B. sericoneura* Liebm.; E, *B. sinuata* Wall.; F, '*B. pretoniensis* Moore'; G, *B. caroliniaefolia* Reg.; H, *B. xanthina* Hook.; I, *B. rhizocarpa* Fisch.—After Fellerer.

definite groups with relatively large areas of unperforated epidermis between them; in other species the stomata are solitary. A **hypoderm** of large water-storage cells is frequently present towards one or both surfaces. The **mesophyll** sometimes contains sclerenchymatous idioblasts which may be crystalliferous. The **petiole** is supplied by isolated vascular bundles, some of which are in the medullary position in certain species. In the **stem** there is a ring of widely spaced **vascular bundles** which are sometimes accompanied by medullary strands, and more rarely by others in the cortex. In the **xylem** the vessels exhibit a characteristic appearance, owing to their having scalariform bordered pits where they are in contact with one another, whilst there are both simple perforations and scalariform plates which often occur together in the end walls. Several kinds of **cystolith** are common in the leaf and occasionally in the stem. **Crystals** are both solitary and clustered, often in the form of octohedra or quadratic prisms.

LEAF

Hairs (Fig. 159) include the following types.

A. *Non-capitate*

Always multicellular, including uniseriate, multiseriate, shaggy, and various other types. Outer cells of the shaggy hairs sometimes with free mamilliform tips, thus resembling cones of one of the Coniferae (Fig. 159 A). Shaggy hairs in other instances consisting only of shortly spinous, star-like structures (Fig. 159 B), or 2-armed. Transitions between shaggy hairs and emergences also occur, these sometimes including sclerenchymatous mechanical cells. Whip-like (Fig. 159 D), stellate (Fig. 159 E) and tufted hairs also recorded.

B. *Capitate* (Fig. 159 F, G, I)

Very variable; the few- or many-celled head being spherical, ellipsoidal, club- or hammer-shaped; stalk also varying in length and structure.

Multicellular, easily detached, shortly stalked **pearl glands** also occur, but usually become detached from herbarium specimens whilst being dried and mounted.

Epidermis on both surfaces usually consisting of large, thin-walled cells; frequently papillose, especially on the upper surface; red cell sap common in the lower epidermal cells. **Cuticle** thin, granular, striate or verrucose. One or many layers of large-celled **hypoderm** occur beneath one or, more frequently, both surfaces in many species; especially well developed and constituting most of the thickness of the leaf in *Begonia fuchsoides* Hook. **Stomata** not numerous, confined to the lower surface, each pair of guard cells surrounded by 3–6 subsidiary cells, often arranged in 2 rings; solitary or in definite groups (Fig. 159 A), the latter often recognizable with the naked eye as white dots. **Hydathodes** occur sporadically on the upper surface near the leaf margin. **Mesophyll** generally including 1 layer of palisade tissue; more rarely consisting of ordinary parenchyma. Palisade cells in some species short and conical, in others elongated and provided with concertina-like foldings of the lateral walls. Assimilatory tissue restricted to a narrow band in the innermost part of the lamina in *Begonia fuchsoides*. Air-filled spaces between the epidermis and palisade cells give a **silvery sheen** to the leaves

of certain species. Stone cells, idioblasts (Fig. 158 B), and similar mechanical elements fairly frequent in the mesophyll or around the veins; palisade cells sometimes locally replaced by stone cells. Ground tissue around the larger **veins** often containing strongly developed collenchyma. Vascular bundles sometimes accompanied by elongated parenchymatous cells. **Petiole**, in transverse sections through the distal end, exhibiting isolated vascular bundles, arranged in a circle in some species, e.g. *B. echinosepala* Reg. (Fig. 154 C), but others, e.g. *B. manicata* Cels. (Fig. 154 F), including medullary strands as well. Outer part of the petiole frequently collenchymatous. **Crystals**, both solitary and clustered, often occurring in the form of single octohedra or quadratic prisms. Several kinds of bodies, resembling **cystoliths** (Fig. 158 C-E), occur in the palisade and spongy tissue of the mesophyll or occasionally in the hypoderm or in the shaggy hairs of certain members of the family; commonly giving rise to transparent dots. Some of these bodies resemble those of *Momordica* (Cucurbitaceae). The following types are recorded by Solereder. (i) Bodies devoid of crystalline infiltration, appearing as white translucent structures in dry sections exposed to the air, but swelling up and forming an apparently structureless mass in water, and subsequently contracting and resembling decalcified double-cystoliths with concentric and radial striations when treated with alcohol. (ii) Bodies exhibiting finely granular structure and yellowish refraction of light in dry sections exposed to the air; turning grey and exhibiting the granular structure and stratification more clearly when treated with water; containing resinous infiltrations soluble in alcohol. (iii) Brittle, strongly refractive, whitish, yellowish, or brownish bodies appearing as gelatinous masses in sections mounted dry or in water, or, in the living plant, as liquid, brightly shining, dull white or yellowish masses of resinous secretion enclosed in special sacs. Similar types of cystolith-like bodies often occur throughout closely related groups of species of *Begonia*, thus serving as a test of affinity, and, to some extent, valuable for specific diagnosis. For further details see Solereder.

AXIS

STEM (Fig. 154 B)

Epidermis consisting of 1-4 layers. **Cork** arising in or immediately below the epidermis. Outer part of the **cortex** collenchymatous; inner part composed of thin-walled tissue containing crystals and chlorophyll; sometimes with red cell sap. **Vascular bundles** appearing, in transverse sections, as a single ring, rarely accompanied by others in the cortex, or, more frequently, in the pith; each bundle subtended on the outer side by elongated parenchymatous cells and by prosenchymatous elements with slit-shaped pits. Bundles of the main ring frequently isolated but sometimes forming a more or less closed ring. Tissue between the bundles, in most shrubby species, consisting of elongated cells with lignified walls and slit-shaped pits; the corresponding tissue in some of the root-climbers is composed of radially elongated or isodiametric, thin-walled cells, forming broad rays similar to those of the Aristolochiaceae. **Xylem** including vessels in radial rows, and progressively larger in diameter towards the exterior of the stem; surrounded by parenchyma. Vessels also provided with scalariform bordered pits where in contact with one another; simple, circular perforations, or scalariform plates with

many bars present in the end walls, both types sometimes occurring together in a single vessel. Tyloses observed in *B. manicata* Cels. Ground tissue of the secondary wood composed chiefly of delicately septate prosenchymatous elements with simple pits. **Pith** composed of large parenchymatous cells with thin, pitted walls.

Pneumatophodes have been described by Vouk (2341) in the stems of *Begonia vitifolia* Schott. where they resemble and replace typical lenticels. The pneumatophodes are composed of (i) an epidermis of small, thin-walled cells devoid of cuticle; (ii) stomata with poorly developed or occluded apertures; (iii) thin-walled photosynthetic tissue with a weakly developed intercellular system which constitutes the main portion of the pneumatophode.

ROOT

The mode of origin of adventitious roots from the cambium in certain species of *Begonia* has been described by Smith (2143).

TAXONOMIC NOTES

Irmscher (1122) has pointed out that the affinities of the family are not well established. It is questionable whether the common occurrence of cystoliths in the Begoniaceae and Cucurbitaceae is of any great taxonomic significance.

ECONOMIC USES

Numerous species of *Begonia* are cultivated for ornamental purposes.

GENUS DESCRIBED

Begonia.*

* Represented in the Kew slide collection.

LITERATURE

On General Anatomy

Irmscher 1122, Knagg 1248, Smith, A. I. 2143, Vouk 2341.

153. DATISCACEAE

(FIG. 160 on p. 696)

SUMMARY

(i) GENERAL

A family which occurs in northern tropical and sub-tropical regions. The species of *Octomeles* and *Tetrameles* are trees, the last genus being characterized by large buttresses. *Datisca*, the remaining genus, consists of shrubs. The anatomy of the family, apart from the wood structure, has not been very fully investigated. Distinctive characters are lacking, but the sclerenchymatous **idioblasts** which, according to Solereder, traverse the entire thickness of the leaf of *Octomeles sumatrana* Miq. are noteworthy.

(ii) WOOD

Vessels large, perforations simple, intervacular pitting alternate, pits to parenchyma conspicuous, simple and irregularly elongated; members of medium length. **Parenchyma** paratracheal, vasicentric to slightly aliform,

storied. **Rays** up to 4-7 cells wide, with few uniseriats, 2-3 stories high, heterogeneous. **Fibres** with small simple pits, very rarely septate, vaguely to distinctly storied; of medium length.

LEAF

Dorsiventral. Shaggy **hairs**, each with a multicellular stalk of variable length, and a spherical or ellipsoidal, multicellular, glandular head, recorded

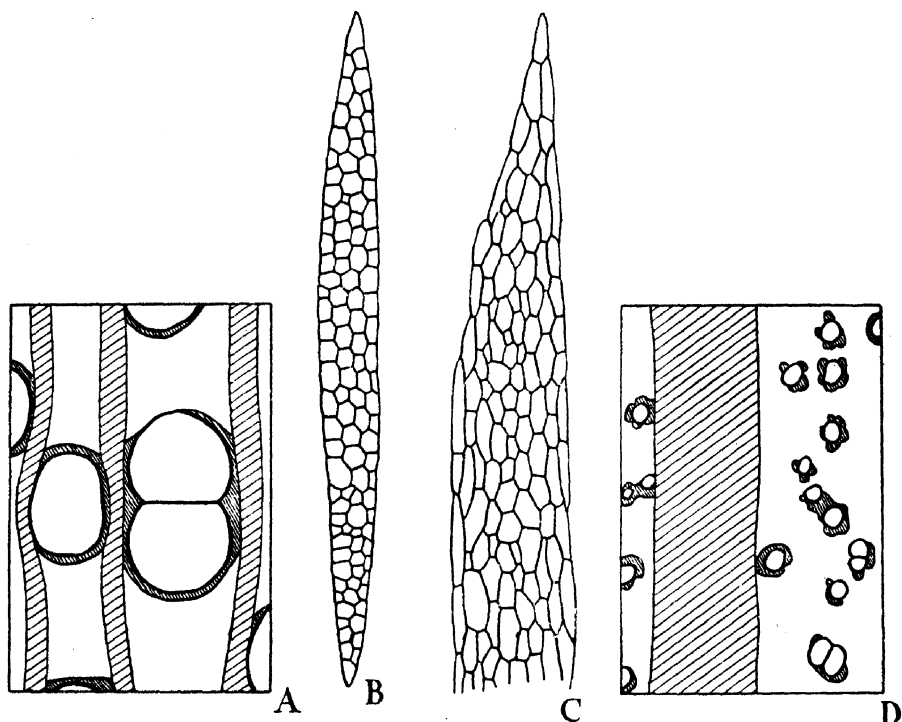


FIG. 160. DATISCACEAE, A-B; CACTACEAE, C-D

A, *Octomeles sumatrana* Miq. B, *O. sumatrana* Miq. C, *Carnegiea gigantea* Britt. et Rose. D, *Lemaireocereus hystrix* Britt. et Rose.

in *Datisca*; scale hairs, each having a 4-seriate stalk bearing a 1-layered, circular shield with an entire margin, present in *Octomeles*. **Stomata** occur on both surfaces in *Octomeles*, although more plentiful on the upper than on the lower side; confined to the lower surface in *Datisca*; ranunculaceous in both genera. A 1-layered **hypoderm** recorded beneath the upper epidermis in *Octomeles*. H-shaped idioblasts, extending from the upper to the lower epidermis, also occur in *Octomeles*. Small prismatic or needle-shaped **crystals** recorded in *Octomeles*.

AXIS

YOUNG STEM

The following details refer to *Octomeles* except where stated. **Cork** composed of relatively thin-walled cells with wide lumina; arising superficially in

material examined at Kew. Branched sclerenchymatous idioblasts and groups of stone cells occur in the pith and/or cortex. **Pericycle** containing a composite and continuous ring of sclerenchyma. Isolated bands of fibres with wide lumina recorded in the corresponding position in *Datisca*. Secondary **phloem** containing groups of fibres except when very young. **Xylem** in young stems exhibiting similar characters to those described below under 'Wood', but rays 1-3 cells wide. Vessels with simple perforations.

WOOD (Fig. 160 A and B)

Vessels large (more than 200 μ mean tangential diameter) or slightly smaller; solitary and in multiples of 2 or 3 cells, occasionally with a slight tendency to an oblique pattern, e.g. in *Octomeles sumatrana* Miq.; mostly 2-4 per sq. mm., though sometimes more numerous locally (up to about 9 per sq. mm.). Perforations simple. Intervascular pitting alternate, medium-sized; pits to ray and wood parenchyma cells typically simple, though Solereder mentions some bordered pitting in *Octomeles*, and with transitions to simple pitting in *Datisca*; large and oblong, elongated horizontally, obliquely or vertically. Tyloses sometimes present, but not abundant. Mean member length 0.4-0.5 mm. **Parenchyma** paratracheal; vasicentric, forming sheaths 1-2 cells thick round the vessels in *Octomeles*, rather more abundant and slightly aliform in *Tetrameles*; scarce in *Datisca* (777). Strands usually of 2-4 cells, occasionally up to 8 cells. Storied. **Rays** up to 4-7 cells wide; both Brown (1679) and Janssonius (1154) refer to the rays as being of 2 sizes; 1 mm. or more high; uniseriates very few in *Octomeles* and *Tetrameles*, small and numerous in *Datisca* (777); composed of square to upright cells; rays usually 3-4 per mm.; heterogeneous (Kribs's Type II B?), with 1-3 marginal rows of upright cells; Janssonius mentions sheath cells in *Tetrameles nudiflora* R. Br. Contents inconspicuous. The multiseriate rays more than 1 story high and the uniseriates too few to be storied. **Fibres** with very small simple pits, mostly on the radial walls; Janssonius refers to septate fibres in a single specimen of *Tetrameles nudiflora*, and Gilg (777) states that the fibres are occasionally septate in *Octomeles*. Walls thin to very thin. Distinctly storied in *Tetrameles* and vaguely so in *Octomeles*. Tapering abruptly and arranged in distinct radial rows. Mean length 0.9-1.4 mm.

ROOT

Tubercles on the roots of *Datisca cannabina* Linn. have been investigated by Severini (2081).

TAXONOMIC NOTES

Although the affinities of the family have been much disputed, it is, according to Gilg (777), generally regarded as related to the Begoniaceae.

ECONOMIC USES

The light, perishable timbers of *Octomeles* and *Tetrameles* are used locally for packing cases. Desch (574) notes that logs of *Octomeles sumatrana* Miq. have been exported to Japan for paper pulp, but that the wood has elsewhere been reported on as unsuitable for this purpose.

GENERA DESCRIBED

Datisca,* Octomeles, Tetrameles.

* Represented in the Kew slide collection.

LITERATURE

(i) *On General Anatomy*

Gilg 777, Severini 2081.

(ii) *On Wood Structure*

den Berger 179, 182, Desch 574, Gilg 777, Howard 1088, Janssonius 1154, Pearson and Brown 1679, Record 1843, 1851.

154. CACTACEAE

(FIG. 160 on p. 696; FIG. 161 on p. 700; FIG. 162 on p. 700)

SUMMARY

(i) GENERAL

A highly specialized family consisting, for the most part, of stem-succulent herbs which usually bear sharp, rigid spines. A few members of the family are definitely shrubby, whilst herbaceous forms may attain a considerable size. The thick succulent stems, in different genera and species, may be cylindrical, fluted, or composed of an aggregation of mammiform portions. Even within a single genus such as *Opuntia* there are dwarf species, tall-stemmed forms with a cylindrical woody axis, and thick-stemmed species with a flattened axis (Reiche 1909). The leaves are usually reduced to scales, so that photosynthesis takes place chiefly in the green stem, except in *Pereskia* which bears typical fleshy leaves. The diverse morphology and anatomy of the vegetative organs have been fully described by Gravis (806), Reiche (1909), Haehnel (862), and Vaupel (2327). Most of the species inhabit desert regions on the American continent, particularly in Mexico, although quite a number, such as the notorious Prickly Pear (*Opuntia*), have become naturalized in other parts of the world. Some species of *Epiphyllum*, *Pereskia*, and *Rhipsalis* occur as epiphytes in moist woodland habitats, while at Kew even some of the desert species have been successfully cultivated for several years in jars of tap water by L. Portheim. The sharp **spines**, whose morphological nature has been much disputed, vary in length and thickness, whilst in some genera they are barbed (so-called **glochidia**). They are usually grouped in small, approximately circular areas (**areoles**) on the surface of the stems. The areoles frequently bear a dense covering of **hairs**, forming a velvet down at the base of the thorns in some species, but in others the hairs are as long as or even longer than the spines, in extreme cases forming a definite flossy coating to the plant. Leinfellner (1345) comparatively recently confirmed the earlier opinion of Goebel and others that, in most genera, the areoles represent short shoots of which the leaves have become metamorphosed to thorns. Boker's (218, 219) still more recent developmental studies on *Opuntia cylindrica* (Lamarck) DC. also confirmed the opinion that 'the areole is best regarded as an axillary bud, growing on a persistent leaf base, and that its appendages should be regarded as the morphological equivalents of leaves. From this it

also follows that spines and glochids can be homologized with bud scales.' In a species of *Pereskia*, Leinfellner noted that a short-lived adventitious root arises from each areole. **Stomata** are more numerous than in typical Dicotyledonous stems, and the orientation of the pore in relation to the long axis of the plant is of taxonomic importance. The collenchymatous outer part of the **cortex** resembles a gelatinous hypoderm of 1 to several layers, usually with pit-like canals connecting the cells. The bulk of the stem is usually composed of mucilaginous ground tissue in which a cylindrical network of vascular bundles is embedded. In only a few species is the outer part of the ground tissue differentiated as palisade. Increase in girth is effected by cell divisions in the ground tissue as well as by cambial activity. **Mucilage cells** in most and **laticiferous canals** in a few genera occur in the ground tissue. Clustered **crystals** of calcium oxalate are often abundant, raphides also occur, but solitary crystals are infrequent. According to Weingart (2386) and Kummer (1301) it is sometimes possible to distinguish closely related species of Cactaceae by microscopical differences in the epidermal cells, stomata and parenchyma. **Anomalous Structure** recorded in a few species.

(ii) WOOD

Vessels small, except in *Pereskia*, solitary and in multiples and clusters, perforations simple, intervascular pitting usually scalariform to opposite, pits to parenchyma similar and often simple; members of medium length to extremely short. **Parenchyma** paratracheal only, a few cells to complete sheaths round the vessels. **Rays** mostly 6-10 cells wide and without uniseriata, often very high, composed almost entirely of square or upright cells. **Fibres** with simple pits, commonly septate, moderately to extremely short. **Tracheids** with an unusual type of spiral thickening present in some genera. Large **radial channels** common.

LEAF

Very much reduced except in *Pereskia*. Rudimentary leaves of *Opuntia* provided with abortive stomata; numerous normal stomata present in *Pereskia*.

AXIS

STEM

Stems generally spiny and in most genera succulent and assuming a variety of forms (see 'Summary' above); constituting the main part of the plant body, and serving as the principal assimilatory organ. **Spines** circular, flattened or angular in transverse section; consisting of a central bundle of thick-walled sclerenchymatous elements surrounded by others with thinner but pitted walls, the whole thorn being covered externally by radial rows of epidermal cells with wide lumina. Glochidia or barbed thorns (Fig. 161 D) with free, imbricate, downwardly projecting points to the epidermal cells also occur, chiefly in *Opuntia*. **Hairs** usually confined to the areoles (see 'Summary'); scanty or short in many species, but in others much longer and more numerous or even forming a definite floss; sometimes unicellular, but mostly uniseriate to multiseriate; component cells short near the bases but larger and broader towards the distal ends of the multicellular hairs, cells sometimes

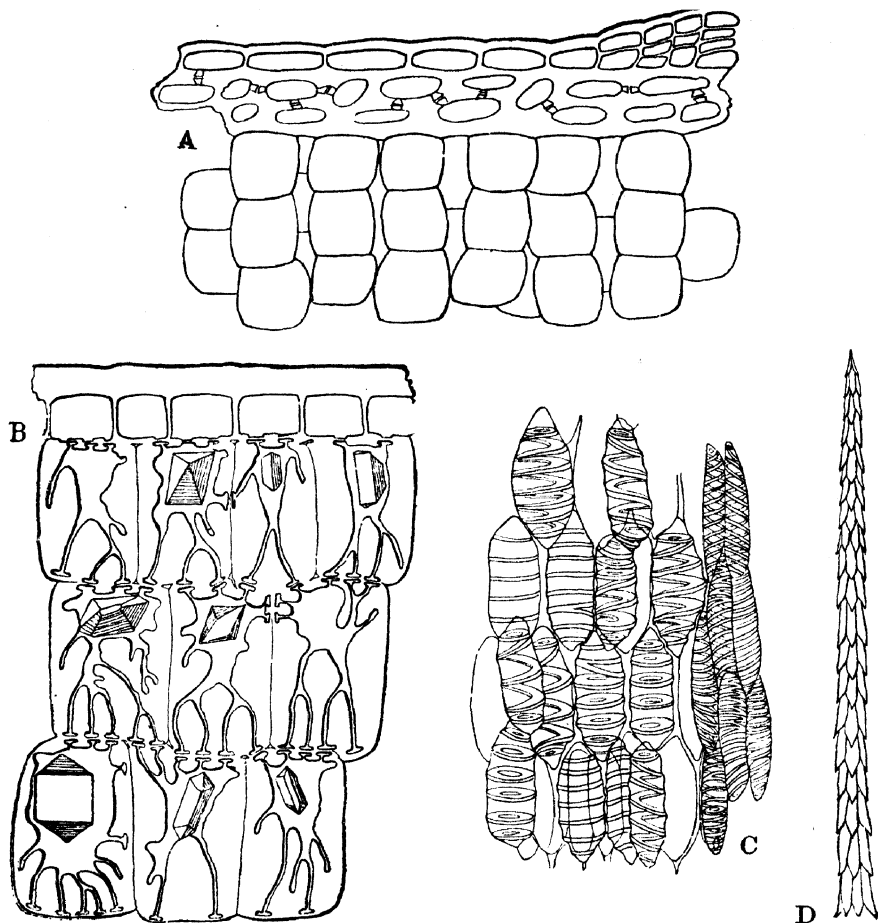


FIG. 161. CACTACEAE

Epidermis and Hypoderm: A, *Cereus variabilis* Pfeiffer. B, *Cactus intortus* Miller. C, Portion of the wood of *Echinopsis eyriesii* (Turpin) Zucc. D, Thorn from the leaf-cushion of *Opuntia ficus indica* (Linn.) Miller.—A-C, after Schleiden, D, by Solereder.

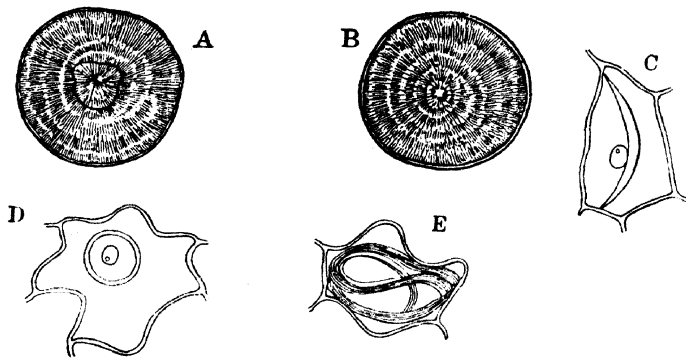


FIG. 162. CACTACEAE

A, B, Sphaerites of '*Phyllocactus* sp.'; C-E, Proteid-bodies; C, in *Schlumbergera russelliana* (Gardner) Britton et Rose; D-E, in *Zygocactus truncatus* (Haworth) Schumann.—A, B after Kohl, C-E after Molisch.

pitted or superficially striate. **Extra-floral nectaries**, secreting a sugary fluid, recorded in species of *Cereus*, *Echinocactus*, *Epiphyllum*, *Neomammillaria*, *Opuntia*, *Rhipsalis*; those of *Epiphyllum* (*Phyllocactus*) stated by Weingart (2387) to originate as abnormal stomata. For mode of secretion see Lloyd and Ridgway (1384). **Cuticle** frequently very thick; sometimes ridged. Surface of the stem often coated with **wax**, which is easily detachable, and described by Vaupel (2327) as sometimes present in sufficient quantities to give a greyish or white colour to young stems, e.g. in *Cephalocereus leucocephalus* (Poselger) Britton et Rose (syn. *Cereus houlletii* (Lem.) Berg.), and *Lemaireocereus pruinosus* Otto (syn. *C. pruinosus* (Pfeiff.) S. Dyck). **Stomata** numerous compared with those in a normal herbaceous stem, but less frequent than in many typical mesophytic leaves; often situated in depressions; with or without subsidiary cells parallel to the pore. Stomatal pores orientated transversely to the long axis of the shoot in species of *Cereus*, *Echinopsis*, *Pfeiffera*, *Rhipsalis*; parallel to the long axis in species of *Epiphyllum*, *Opuntia*, *Rhipsalis*; irregularly orientated in species of *Echinocactus*, *Epiphyllum*, *Neomammillaria*. Stomata in certain members of the family become closed by the development of thylloid cells, with or without thickenings, which according to Bukvic (307) arise from the subsidiary cells and/or those of the mesophyll. Long, tubular, respiratory cavities beneath the stomata sometimes perforate the sub-epidermal collenchyma. A collenchymatous, mucilaginous, **pseudo-hypoderm** (Fig. 161 A-B) of 1 to several layers of cells recorded in certain genera including *Cactus*, *Cereus*, *Echinocactus*, *Echinopsis*, *Opuntia* (Nommeusen 1604); sometimes consisting of 6-7 layers in *Echinocactus* or 12-14 in *Cereus*; the component cells interconnected by branched or unbranched, pit-like canals. Hypoderm not well developed in *Ariocarpus*, *Epiphyllum*, and *Pereskia*. **Cork** arising in the epidermis, hypodermis, or ground tissue; sometimes forming unsightly patches on the surface of the plants, especially, according to Bukvic (307), when grown in unfavourable conditions. For further particulars of cork development, including the formation of intumescences in *Epiphyllum* (*Phyllocactus*) see Nommeusen (1604), Heinricher (942), Wolff (2450), and, for wound cork in *Opuntia*, Coutant (487). Ground tissue composed chiefly of spherical cells, usually interspersed with well-developed intercellular spaces except near the epidermis and in the primary rays; including thick-walled cells in many species of *Rhipsalis*. Outer part of the ground tissue constituting the chief assimilatory region, but only rarely differentiated as palisade, e.g. according to Solereder in *Carnegiea gigantea* (Engelm.) Britton et Rose (syn. *Cereus giganteus* Engelm.). Inner part of the ground tissue composed of cells with copious, mucilaginous contents.

The cells of the ground tissue remain meristematic for a long time, and, by dividing, contribute largely to the increase in girth of the axis. This persistent meristematic power also enables the Cactaceae to be readily propagated from cuttings or by grafting on other members of the same family.

The vascular network, in transverse sections of most members of the Cactaceae, appears as a principal ring of separate **vascular bundles**, accompanied, in some species, by additional strands in the cortex, and, less frequently, the pith. Vessels with simple perforations. **Medullary bundles** recorded in *Trichocereus candicans* (Gillies) Britton et Rose as well as in species of *Echinocactus*, *Echinopsis*, *Neomammillaria*, but not in *N. mammillaris* (L.) Britton et

Rose and *N. glochidiata* (Mart.) Britton et Rose. **Cortical bundles**, according to Solereder, arranged in 2 rows in the angles in *Rhipsalis crispata* (Haworth) Pfeiffer, *R. pachyptera* Pfeiffer, and *R. rhombea* (Salm-Dyck) Pfeiffer; in all of the angles and sometimes between them in *R. micrantha* (H.B. et K.) DC., *R. paradoxa* Salm-Dyck, *R. pentaptera* Pfeiffer; situated chiefly in the angles in *Lepismium cruciforme* (Vellozo) Miquel and *Pfeiffera ianthothele* (Monville) Weber. Cortical bundles arranged in small, usually circular groups in *Hattiora salicornioides* (Haw.) Britton et Rose and in the following species of *Rhipsalis*: *R. cassutha* Gaertn., *R. cereuscula* Haw., *R. cribrata* (Lem.) Rümpler, *R. floccosa* Salm-Dyck., *R. grandiflora* Haw., *R. mesembryanthemoides* Haw., *R. teres* (Vellozo) Steudel. Mechanical support for the main cauline ring of bundles is provided by thickened elements at the outer periphery of the phloem in the large but not in the small species. Bundles of the main vascular ring remain separate for a long time before becoming connected to form a continuous cylinder following the formation of interfascicular cambium. **Xylem** constituting a large proportion of the axis in *Pereskia*. **Laticiferous canals** with white, fairly dense, fluid contents, which sometimes harden and turn yellow, present in *Coryphantha macromeris* (Engelm.) Lemaire, *Leuchtenbergia principis* Hook., and many species of *Neomammillaria*. Contents of the canals consisting of a mixture of resin and rubber-like material, soluble in chloroform and ether and stained bright red by tincture of alkannin. Canals isolated when present in the inner part of the plant, but more numerous and anastomosing in the cortical parenchyma, extending outwards to the inner boundary of the sub-epidermal collenchyma. **Crystals** of calcium oxalate very numerous, usually clustered, the clusters in *Opuntia* being stellate or irregular. Raphides recorded in *Malacocarpus ottonia* Lehmann and in *Opuntia* spp., and sphaerocrystals (Fig. 162 A-B) locally in *Coryphantha octacantha* DC., *Neomammillaria wildii* (Dietrich) Britton et Rose, '*Phyllocactus*', *Selenicereus hamatus* (Scheidw.) Britton et Rose, *S. pteranthus* (Link et Otto) Britton et Rose. Sphaerocrystalline masses of unidentified material reported to occur in specimens preserved in alcohol. Crystalliferous cells scattered in many species, but concentrated in a sub-epidermal layer in others, both arrangements occurring in different species of a single genus in some instances. Mucilage cells sometimes accompany the crystalliferous cells.

For details concerning the deposition of mucilage see Stewart (2200). Cortical mucilage cavities also occur in species of *Opuntia*. According to Reiche (1911) mucilage, extruded from damaged areoles and other wounds in *Opuntia tomentosa* Salm-Dyck, is at first a yellowish-brown fluid but becomes hard and brittle.

The following arrangements of crystalliferous and mucilaginous cells are recorded for certain species of the genera mentioned.

- I. Scattered crystalliferous cells, unaccompanied by mucilage cells in *Ariocarpus*, *Coryphantha*, *Dolichothele*, *Echinocereus*, *Echinopsis*, *Neomammillaria*, *Pereskia*, *Pfeiffera*.
- II. Crystalliferous cells arranged in a definite sub-epidermal layer, not accompanied by mucilage cells, in *Astrophytum*, *Echinocactus*, *Neomammillaria*, *Opuntia*, *Pelecypora*, *Pereskia*.
- III. Scattered mucilaginous and crystalliferous cells occur together in

Cereus, *Echinocereus*, *Echinopsis*, *Epiphyllum*, *Gymnocalycium*, *Lepismium*, *Malacocarpus*, *Pereskia*, *Pfeiffera*, *Rhipsalis*.

- IV. A sub-epidermal layer of mixed mucilaginous and crystalliferous cells in *Coryphantha octacantha* (DC.) Britton et Rose and *Opuntia subulata* (Muhl.) Engelm.

Curiously shaped '**proteid bodies**' (Fig. 162 C-E) recorded by Solereder in the epidermis and adjacent parenchyma of *Schlumbergera* and *Zygocactus*. **Saponin** said to occur in *Cereus*.

ETIOLATED SHOOTS

Etiolated shoots of *Opuntia* have been described by Brown (290) as differing from the normal in the following respects. Cuticle absent. Surface becoming covered with small papillae each provided with an apical stoma. Normal stomata less numerous. Hypoderm of pitted cells, palisade tissue, and sub-epidermal crystalliferous layer not developed. Air cavities reduced. Etiolated shoots, when placed in normal light, lose the stomata at the apices of the papillae by decortication.

WOOD (Figs. 160 C and D and 161 C)

Vessels mostly very small (25-50 μ mean tangential diameter), rather larger in *Carnegiea*, and medium-sized (100-200 μ) to large in *Pereskia*; solitary, in small multiples and irregular groups or clusters; with a tendency to a tangential arrangement in *Cereus* (1894), mostly 10-30 per sq. mm., fewer in *Pereskia*; sometimes semi-ring-porous in *Cereus*. Perforations typically simple, but with a few irregularly reticulate plates in *Harrisia*. Intervascular pitting typically scalariform to opposite, the pits with wide apertures and narrow borders; pits round and intermediate between opposite and alternate, or with no very obvious arrangement in *Cereus*; pits to parenchyma similar in shape and distribution and simple. Contents not observed. Mean length 0.1-0.5 mm. **Parenchyma** typically paratracheal and rather sparse; vasicentric or only partly enclosing the vessels, sometimes tending to link together groups of vessels in *Carnegiea*, *Cereus*, and *Pereskia*, and occasionally forming broad bands in the latter; diffuse parenchyma reported (533) as sometimes present. Strands usually of 2-4 cells. **Rays** mostly up to 6-10 cells wide, sometimes more than 10 cells wide in *Carnegiea* and *Pereskia*; often several millimetres high, but with various degrees of dissection into shorter units; uniseriate rays absent; mostly 2-3 rays per mm.; typically composed almost entirely of square to slightly upright cells, with marginal rows of high upright cells; with some procumbent cells in *Neoabbottia*; sheath cells often present. With occasional druses in *Cereus*, *Dendrocereus*, *Leptocereus*, and *Pereskia*. Strands of small tracheid-like vessels observed in a few rays in 1 specimen of *Leptocereus*. **Fibres** with simple pits, more numerous on the radial than on the tangential walls. Septate in *Cereus*, *Harrisia*, *Lemaireocereus*, *Leptocereus*, *Neoabbottia*, *Nopalea*, and *Pereskia*. Walls moderately thin to thick. Mean length 0.4-0.9 mm. **Tracheids**. According to Schleiden, as quoted by Solereder, the wood of most of the *Opuntias* and of *Cactus*, *Echinocactus*, and *Neomammillaria* is characterized by elementary organs of quite a special nature (Fig. 161 C); these are broad cells with very thin walls,

in shape midway between that of a barrel and that of a spindle; they are provided with locular or spiral thickening ridges, which are inserted on the thin wall by their narrow edge, and project far into the cell lumen. Generally these tracheids are also distinguished from the actual vessels by lack of perforations, but in *Echinocactus* and *Mammillaria* rows of such cells occur connected by perforations. In *Opuntia* these cells are absent from some species, particularly those with flat oval shoots of the type of *Opuntia ficus indica* (L.) Miller; in some species they occur sparingly in the articulations between the segments, quite apart from the vascular bundles, in the rays or at the margins of the pith; in others they are an integral part of the bundles. They are found in larger quantities in *Echinocactus* and *Melocactus*, where, except in the lowest internodes, they form the most important part of the xylem. In certain species of *Neomammillaria* all elements other than the tracheae of the primary xylem disappear and these cells form the bulk of the xylem. Solereder also quotes Preston as stating that in *Cereus fendleri* Engelm. similar cells occur in broad zones alternating with narrow zones of spiral vessels. **Intercellular canals.** Radial channels often present, giving a pitted appearance to the tangential surface of the wood (1886).

ANOMALOUS STRUCTURE

Anomalous secondary thickening recorded in *Rhipsalis* by Milanez (1523) and *Echinofossulocactus multicostatus* (Hildm.) Britton et Rose (syn. *Echinocactus multicostatus* Hildm.) by Haehnel (862).

ROOT

Roots generally narrow and woody compared with the stem; tap roots sometimes well developed, e.g. the fleshy roots in certain species of *Neomammillaria*. Tuberous roots present in *Peniocereus greggii* (Engelm.) Britton et Rose (syn. *Cereus greggii* Engelm.) and species with thin stems, e.g. *Wilcoxia poselgeri* (Lemaire) Britton et Rose (syn. *Echinocactus tuberosus* Rump.) the rat's tail cactus. String-like roots a yard long recorded in *Opuntia*. Swollen roots covered with cork and filled with mucilaginous internal tissue. Xylem and phloem strands in the lateral roots of *Echinofossulocactus multicostatus* (Hildm.) Britton et Rose (syn. *Echinocactus multicostatus* Hildm.) opposite and not alternate as in most roots. Roots in the same species covered with cork but devoid of mucilage cells. Anchoring roots of epiphytic species originate near the central vascular cylinder of the aerial axis, and grow out through the cortical ground tissue. Anchoring roots of *Selenicereus hamatus* (Schweidw.) Britton et Rose (syn. *Cereus hamatus* Scheidw.) octarch, but those of certain other epiphytic species ribbon-shaped and polyarch. All of the above information is recorded by Haehnel (862). The following particulars recorded for *Neomammillaria* by Hemenway and Breazeale (948). Hairs present when young but disappearing when older; cork occurring on old roots; xylem including spiral thickening and thin cellulose walls. Contractile roots of *Echinocactus* said by Nommensen (1604) to become split by enlarged groups of wound cork. Laticiferous canals present in the roots of those species in which they have been recorded in the stem (see 'Stem' on p. 702). Secondary thickening in the root of *Rhipsalis* has been described by Milanez (1523).

TAXONOMIC NOTES

It is not easy to establish the affinities of such a specialized group as the Cactaceae. Chorinsky (408) noted that the structure and mode of origin of the emergences in *Pereskia* and *Rhipsalis* resemble those of the emergences of *Anacampseros* (Portulacaceae), and claimed this as additional proof of the existence of affinities between the Cactaceae and Portulacaceae. Wettstein (2416) has also drawn attention to the floral and anatomical similarities between the Cactaceae and other families included in the Centrospermae. Britton and Rose's monograph (275) has become the standard work on the general taxonomy of the Cactaceae, and in the present account the nomenclature of those authors has been followed as closely as possible.

ECONOMIC USES

The fruits and succulent stems, especially of *Opuntia*, have been used as fodder in dry countries. The dead bodies of certain scale insects which infest species of *Opuntia* and *Nopalea* yield the red dye cochineal. The Prickly Pear (*Opuntia* and *Nopalea* spp.) has become a very serious weed in certain parts of the world to which it has been introduced, notably in parts of Australia (see Shirley and Lambert (2090)). The thorns of Prickly Pear and possibly of other Cactaceae are used as gramophone needles. An extract of *Selenicereus grandiflorus* (L.) Britton et Rose (syn. *Cereus grandiflorus* Mill.) has been used as a heart stimulant, but its therapeutic value is not well established. Rouhier (1961) has described the use of certain members of the family by Mexican Indians for ritual purposes, and also states that some Cactaceae influence the nervous system through the action of the alkaloids which they contain. The distribution of alkaloids in a species of *Echinocactus* has been investigated by Steiner-Bernier (2193). Many members of the family are commonly cultivated on account of their unusual and frequently grotesque appearance.

The wood, according to Record and Hess (1886), is sometimes considerably used locally owing to the scarcity of other timber. The Cardón, *Cereus* or *Cephalocereus*, in parts of northern Venezuela supplies attractive, easily worked timber for furniture and general construction.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Ariocarpus, Astrophytum, Carnegiea, Cephalocereus, Cereus, Coryphantha, Dolichothele, Echinocactus, Echinocereus, Echinofossulocactus, Echinopsis, Epiphyllum, Gymnocalycium, Hatiora, Lemaireocereus, Lepismium, Leuchtenbergia, Malacocarpus, Neomammillaria, Nopalea, Opuntia, Pelecyphora, Peniocereus, Pereskia, Pfeiffera, Rhipsalis, Schlumbergera, Selenicereus, Trichocereus, Wilcoxia.

(ii) FOR WOOD STRUCTURE

(Cactus), Carnegiea, Cephalocereus, Cereus, Dendrocereus, (Echinocactus), Harrisia, Lemaireocereus, Leptocereus, Neoabbottia, Neomammillaria, Nopalea, (Opuntia), Pereskia.

LITERATURE

(i) *On General Anatomy*

Bedelian 166, Boke 218, 219, Britton and Rose 275, Brown, J. G. 290, Bukvic 307, Chorinsky 408, Coutant 487, Dauman 545, Gravis 806, Haehnel 862, Heinricher 942, Hemenway and Breazeale 948, Jeffrey and Cole 1167, Kummer 1301, Leinfellner 1345, Lloyd and Ridgway 1384, Markgraf 1441, 1442, Milanez 1523, Nommeusen 1604, Pfeiffer, H. 1707, Reiche 1909, 1911, Rouhier 1961, Scaramella 2026, Shirley and Lambert 2089, 2090, Steiner-Bernier 2193, Stewart 2200, Vaupel 2327, Weingart 2386, 2387, Wettstein 2416, Wolf 2450.

(ii) *On Wood Structure*

Burgerstein 312, Cozzo 494, Dadswell and Record 533, Kanehira 1209, Milanez 1523, Record 1781, 1787, 1843, 1851, Record and Hess 1886, Record and Mell 1894, Tupper 2295.

155. FICOIDACEAE

(FIG. 163 on p. 708)

SUMMARY

Mostly succulent herbs, but a few genera tend to be shrubby. The family occurs chiefly, but not exclusively, in desert regions in the tropics and subtropics, reaching its maximum development in South Africa and Western Australia. The leaves usually constitute the most fleshy part of the plant, and, in very specialized members of the family such as *Lithops* and *Lapidaria*, the aerial part of the plant consists of opposite fleshy leaves between which the flowers arise. These remarkable members of the family strongly resemble the desert stones amongst which they grow. The family also includes species with reduced leaves, the main part of the plant then consisting of assimilatory branches, the habit resembling that of species of *Cytisus*. Others are more like *Salicornia*. The **epidermis** of both leaf and stem generally includes large, bladder-like cells, which suggest the name 'ice-plants' which is sometimes applied to members of the family. The **stomata** are generally ranunculaceous, but, in a few instances, rubiaceous. The **mesophyll** of the leaves is most frequently centric, but there are numerous exceptions. It usually consists wholly of palisade cells, but there is frequently a core of aqueous tissue in which the vascular system is embedded. The aqueous tissue extends to the epidermis at the apex of leaves of the type found in *Lithops* which has caused these organs to be termed 'window' leaves (Fensterblätter). The leaves sometimes exhibit a characteristically chalky appearance due to the deposition of small **crystals** in the epidermis. The most noteworthy features of the **axis** are the common occurrence of **anomalous secondary thickening** in both stem and root, the frequent presence of a reticulum of **leaf trace bundles** in the cortex, and the infrequency of rays in the xylem. **Secretory elements** are known only in the form of large tannin sacs in a few species of *Mesembryanthemum*.¹ **Crystals** solitary, in clusters, or in the form of raphides.

LEAF

Nearly always centric; with or without a central core of aqueous tissue, but relatively flat leaves isobilateral, e.g. in *Sesuvium portulacastrum* Linn. Iso-

¹ For the sense in which the name *Mesembryanthemum* is used in this book see 'Taxonomic Notes' on p. 711.

bilateral leaves also recorded by Sabnis (1977) in species of *Limeum*, *Mollugo*, *Orygia*, and dorsiventral ones in *Gisekia*, *Mollugo*, *Trianthema* (see also 'Mesophyll' on p. 709). Surface sometimes coated with **wax**. **Hairs** simple, unicellular in certain species of *Mesembryanthemum*; unicellular, 2-armed in species of *Aizoon*, *Galenia*, *Plinthus*; each having a uniseriate stalk bearing a unicellular, stellate head in species of *Glinus* (Fig. 163 c). Leaf tips of species of *Trichodiadema* provided with cork cushions bearing a cluster of hairs or papillae according to Oberstein (1926). Glandular hairs with a 1- or 2-celled stalk and a large globular head, situated in small depressions on both surfaces of the leaf recorded by Pilger (1920) in *Glischrothamnus ulei* Pilger. A dense covering of stellate hairs also recorded by Sabnis (1977) in *Mollugo hirta* Thunb. **Epidermis** composed of large, bladder-like, water-storage cells intercalated between much smaller ones, in species of *Aizoon* (Fig. 163 B), *Cryophytum* (Fig. 163 A), *Galenia*, *Mesembryanthemum*, *Sesuvium* (enlarged cells not seen by Mullan (1571) in plants of *S. portulacastrum* Linn. growing on the sea-shore), *Tetragonia*, *Trianthema*; the large cells sometimes provided with hair-like or papillose extensions, e.g. in species of *Mesembryanthemum* and *Tetragonia*. Epidermis, in a few species of *Hereroa* examined by Zemke (2505), consisting wholly of small cells, the latter being protected externally by a thin layer of cuticle. Reule (1925), who examined 81 species of *Mesembryanthemum* (*sensu lato*) collected in South Africa and cultivated in Germany, found the structure of the epidermis and stomata to provide features of considerable taxonomic interest. He recognized 7 more or less distinct types of epidermis connected by transitional forms. **TYPE I** (Normal Type). Epidermal cells isodiametric, polygonal, outer wall at most slightly sinuous when viewed in transverse sections, and, at most, projecting only slightly into the sub-epidermal layer. Thickness of cuticle 3–17 μ . Type I observed in species of *Bergeranthus*, *Carruanthus*, *Chasmatophyllum*, *Cheiridopsis*, *Conophyllum*, *Conophytum* (few species only), *Faucaria*, *Fenestraria*, *Gibbaeum*, *Glottiphyllum*, *Nananthus*, *Pleisopilos*, *Rhombophyllum*, *Semnanthe*. **TYPE II** (Conophytum Type). Epidermal cells covered externally by a very thick, flat, continuous layer of cuticle, the latter extending over the whole surface except where interrupted by the stomata. In general similar to Type I but with much thicker cuticle. Type II observed in species of *Argyroderma*, *Conophytum* (10 spp.), *Ruschia*. **TYPE III** (Lithops Type). Epidermal cells protected externally by a thick layer of cuticle, the latter tending to form rounded, blunt papillae over the individual epidermal cells. Cuticle more definitely papillose in some genera than in others. Type III observed in species of *Conophytum* (1 sp.), *Corpuscularia*, *Lapidaria*, *Lithops* (6 spp.), *Rimaria*. **TYPE IV** (Kegellzellentypus). Similar to Type III, but outer walls of the epidermal cells provided with more pointed cuticular papillae. Type IV observed in certain species of *Cheiridopsis*. **TYPE V** (Cheiridopsis Pilansii Type). Cuticle deposited in the form of hair-like structures on the outer walls of the epidermal cells. Type V observed in certain species of *Cheiridopsis* and *Gibbaeum*. **TYPE VI** (Riesenzellentypus). Some of the epidermal cells very much enlarged compared with the remainder. Type VI observed in species of *Delosperma* and *Trichodiadema*. **TYPE VII**. A proportion of the epidermal cells united in groups which are collectively much larger than the remaining epidermal cells. Type VII observed in *Odontophorus* and *Psammotropha*.

Reule also found the stomata to vary in structure and the extent to which they are sunk in the leaf tissue, species resembling one another in epidermal structure also exhibiting similar stomata. The types of epidermal structure enumerated above tend to correspond to the genera, but it will be noted that there are discrepancies. Thus in some of the genera, e.g. *Conophytum* and *Lithops*, the epidermal structure was frequently of a uniform type in most but not all of the species available for examination. Other genera included species

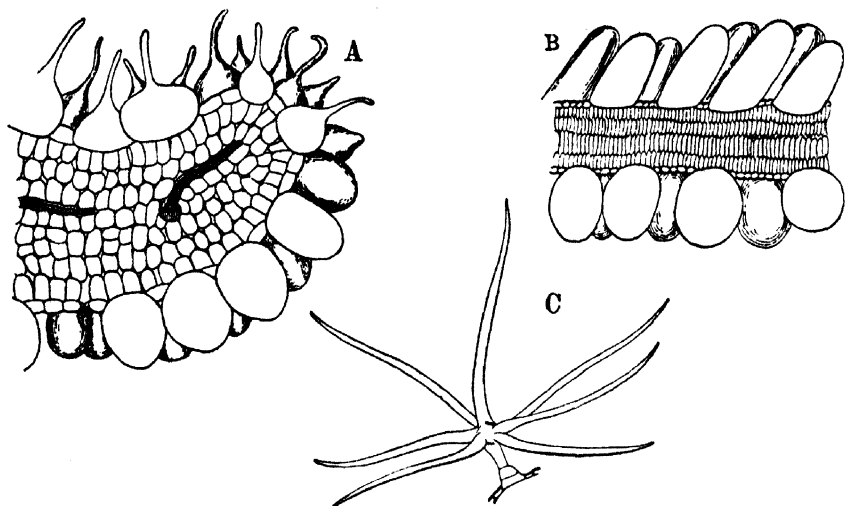


FIG. 163. FICOIDACEAE

A, Transverse section through the margin of the leaf of *Cryophytum crystallinum* (L.) N. E. Br. B, Transverse section through the leaf of *Aizoon canariense* L. C, Stellate hair of *Glinus cambedesii* Fenzl.—A, B after Volkens, C by Solereder.

each showing a different type of epidermal structure, e.g. in *Ruschia*. Finally Reule noted some correspondence between epidermal structure and dryness of habitat, but the ecological significance of this could not be fully assessed without further physiological experiments.

Reule's results could be only partly confirmed by Oztig (1648), who found the structure of the epidermal cells to vary in plants of a single species from different localities or even in different parts of a single leaf. According to Oztig the cuticle of the leaf epidermis is nearly always very thin, and seldom striated. In extreme xerophytic forms such as species of *Conophytum* and *Lithops* the epidermal cells are strongly thickened in a peculiar way, cutinized lamellae of cellulose being present below the cuticle itself. The cutinized layers sometimes extend to the lateral walls, especially in *Lithops*, and appear wedge-, top-, rod-, or spindle-shaped in transverse sections. In some species of *Conophytum* and *Lithops* they extend inwards from the outside wall, forming a lens or peg in the centre of the cell. Unlike Reule, Oztig was unable to observe complete cutinization of the outer wall of the cell. **Stomata** somewhat variable; orientated transversely to the longitudinal axis in some but not all species of *Mesembryanthemum*; said to be ranunculaceous in species of *Adenogramma*, *Gisekia*, *Limeum*, *Mesembryanthemum*, *Polpoda*, *Psammotropha*,

Tetragonia, but rubiaceous in other species of *Mesembryanthemum*. **Mesophyll.** Palisade tissue in *Trianthema portulacastrum* Linn. said by Kienholz (1236) to be confined to the centre of the mesophyll, especially around the veins. Sabnis (1977) also records the occurrence of green bundle sheaths in certain species of *Mollugo* and *Trianthema*. Palisade tissue in *Trianthema triquetra* Rottl. et Willd. said by Sabnis to be confined to arcs of tissue towards the lower surface, the remainder of the mesophyll in this species consisting of aqueous tissue. Pax and Hoffmann (1675) cite Brenner as having recorded the occurrence, in *Lampranthus curvifolius* (Haw.) N. E. Br., of a circle of small bundles on the inside of 3-5 layers of palisade tissue, the main vascular strand being embedded in the central core of water-storage tissue. The small outer bundles in the same species are continuous with 2 lateral strands given off from the central bundle near the base of the leaf. **'Window' leaves** (Fensterblätter), in which aqueous tissue replaces the chlorenchyma at the distal ends, recorded by Brown, Tischer, and Karsten (293) in all species of *Fenestraria* and *Lithops*, in certain species of *Conophytum* and in the monotypic genera *Frithia* and *Imitaria*.

The physiological significance of 'window' leaves has been investigated by Huber (1104), Kean (1226), and Schmucker (2042). Contrary to previously accepted views, Schmucker demonstrated that, in spite of the absence of stomata, the 'window' tissue is the chief transpiratory surface of the leaf, loss of water occurring via the cuticle, and reaching a maximum in damp air and at an average temperature. Furthermore, sinking the plant deeply in a sandy substratum accelerates transpiration. The intensity of the light reaching the inner surface of the cylinder of assimilatory tissue through the 'window' is sometimes reduced, e.g. in *Lithops pseudotruncatella* (Berg.) N. E. Br. by deposits of calcium oxalate on the surface, and, in *Hypertelis*, *Orygia*, &c., by a waxy coating.

Large **tannin sacs** occur below the epidermis in a few species of *Mesembryanthemum* according to Oberstein (1627). The translucent, mucilaginous tanniniferous cells sometimes serve as **lens cells** according to Kean (1226). Lens cells in the epidermis also described by Summers (2221). Small **crystals** in the epidermal cells of *Mesembryanthemum* sometimes give the leaves a white, chalky appearance. Outer walls of the epidermal cells in *Mesembryanthemum* more or less encrusted with calcium oxalate crystals according to Oztig (1648). Encrustation most strongly developed and individual crystals especially large in extreme xeromorphic species. Large cluster crystals embedded in the outer walls of the epidermal cells in a few species, e.g. of *Lapidaria* and *Lithops*. Amount of crystalline deposit said to vary according to the intensity of light to which the leaf is exposed. Crystals rarely present in the inner and anticlinal as well as in the outer walls of the epidermal cells. Solitary crystals recorded by Solereder and other authors in *Adenogramma*, *Coelanthium*, *Cypselea*, *Polpoda*; clusters in *Glinus*, *Hypertelis*, *Limeum*, *Mollugo*, *Orygia*, *Pharnaceum*, *Sesuvium*, *Trianthema*; raphides in *Gisekia*, *Mesembryanthemum*, and *Mollugo*; crystal-sand in *Hypertelis acida* (Hook.) K. Mull. Cubical crystals of calcium phosphate and spherical crystals of calcium malate recorded by Kean (1225) in spirit material of *Mesembryanthemum*. Oxalic and malic acids said to occur in *Mesembryanthemum*, and malic, citric, and phosphoric acids in *Cryophytum crystallinum*

(L.) N. E. Br. Reddish-brown colour of the leaves of certain species of *Aloinopsis* and *Lithops* found by Oztig (1648) to be due to orange-coloured **chromoplasts** in the epidermal and sub-epidermal cells as well as to anthocyan pigments mostly in the sub-epidermal cells. Contrary to earlier statements in the literature, Oztig found no reddish-brown cystoliths. Colour in *Conophytum* mainly due to anthocyan alone.

AXIS

STEM

Epidermis in *Mesembryanthemum* including bladder-like aqueous cells similar to those of the leaf. **Cork** arising in the inner part of the cortex in the few species of *Mesembryanthemum* in which its formation has been examined. Outer part of the primary **cortex** sometimes differentiated as assimilatory tissue. Zemke (2505) refers to an **endodermis** in '*Mesembryanthemum salicornioides*' which becomes suberized at an early stage, a phellogen subsequently arising on the inside of the layer of endodermal cells. **Pericycle** either devoid of sclerenchyma, e.g. in *Trianthema pentandra* Linn., or including stone cells, e.g. in species of *Limeum*, *Mollugo*, *Orygia*. A reticulum of cortical **leaf trace bundles** also frequent in *Mesembryanthemum*. **Xylem** including vessels with bordered pits and simple perforations embedded in ground tissue, the latter usually consisting of prosenchymatous elements with simple pits, but including a varying proportion of parenchyma. Delicate spiral thickening of the vessel wall recorded in *Galenia*. Medullary rays generally absent but present in *Gisekia*, *Macarthuria* (relatively broad), *Orygia* (narrow). **Crystals** include (i) raphides, sometimes in suberized sacs, in the ground tissue of *Mesembryanthemum*; (ii) styloids in the phloem of *Aizoon* sp. and in the pith of *Tetragonia spicata* Linn.; (iii) clusters in the cortex of *Limeum*, *Mollugo*, *Sesuvium portulacastrum* Linn., and *Tetragonia expansa* Murr. See also under 'Leaf' on p. 706.

ROOT

Cortex lacunar in *Sesuvium portulacastrum* Linn. according to Mullan (1571). For normal and anomalous secondary thickening see 'Anomalous Structure' below.

ANOMALOUS STRUCTURE

Anomalous structure common in both stem and root especially in woody species, caused by the development of secondary bundles from successive rings or arcs of meristem in the phloem or pericycle. (A) Stems. Two main types of anomaly recognized. (i) Numerous bundles arranged in more or less distinct concentric rings, embedded in prosenchymatous ground tissue in many species of *Mesembryanthemum* as well as in a few of *Acrosanthes*, *Galenia*, *Macarthuria*, *Sesuvium*, *Trianthema*. (ii) Alternating, more or less complete rings of xylem and phloem in species of *Aizoon*, *Glinus*, *Limeum*, *Orygia*, *Pharnaceum*, *Sesuvium*, *Tetragonia*, *Trianthema*. Transitions between (i) and (ii) also occur. Anomalous thickening in a special zone above the root described by Schmid (2035) in *Lithops pseudotruncatella* (Berg.) N. E. Br. (*Mesembryanthemum pseudotruncatellum* Berg.). Secondary thickening said to be normal in the herbaceous genera *Adenogramma*, *Gisekia*, *Limeum*, *Psammo-*

tropa, and in the woody genus *Polpoda*. (B) Roots. Anomalous thickening recorded in species of *Mesembryanthemum* as well as in *Aizoon hispanicum* Linn., *Mollugo radiata* Ruiz. et Pav., *Sesuvium portulacastrum* Linn., *Tetragonia expansa* Murr. Normal thickening stated to occur in *Pharnaceum incanum* Linn. and *Psammotropa quadrangularis* (L.) Fenzl.

ECONOMIC USES

No important economic products are obtained from this family, but many of its members are cultivated on account of their unusual morphology or for their beautiful flowers. A few species have been used as vegetables, for example, according to Zwicky (2512) by Hottentots in the South African Karoo.

TAXONOMIC NOTES

Certain members of the Ficoidaceae resemble the Centrospermae sufficiently to suggest that their affinities lie in this direction. This is, to some extent, confirmed by similarities in the anatomical structure, particularly by the widespread occurrence of anomalous secondary thickening. In this connexion Pax and Hoffmann (1675) particularly emphasize the resemblances between the Ficoidaceae and Phytolaccaceae, but also point out that considerable differences exist between the Ficoidaceae and Cactaceae.

Considerable difficulties have arisen in recent years concerning the taxonomy of *Mesembryanthemum*, which has been split into numerous genera by N. E. Brown (291), Schwantes (2057), and L. Bolus (222). Owing to the lack of general agreement between those authors there has been much confusion. Pax and Hoffmann (1675) in the main follow N. E. Brown, but also retain the genus *Mesembryanthemum* in a wide sense. K. von Poellnitz (*Repert. Nov. Regn. Veg.* 32, 1933, and *Monatschr. Kakteenkunde*, 1933) has attempted to clear up the existing confusion. Owing to the difficulty of correlating the old species names under *Mesembryanthemum* with their modern synonyms, it has been necessary, in the present book, to follow Pax and Hoffman in retaining the name *Mesembryanthemum* in a wide sense. This has been done when citing information recorded in the literature. Whenever possible, however, the names given to the species by N. E. Brown have been used, as these are generally accepted by British and German investigators. A complete anatomical revision of the family could usefully be undertaken as soon as the taxonomy of the family is more stable.

GENERA DESCRIBED

Acrosanthes, Adenogramma, Adenostemma, Aizoon, Aloinopsis, Argyroderma, Bergeranthus, Carruanthus, Chasmatophyllum, Cheiridopsis, Coelanthium, Conophyllum, Conophytum, Corpuscularia, Cypselea, Delosperma, Faucaria, Fenestraria, Frithia, Galenia, Gibbaeum, Gisekia, Glinus, Glischrothamnus, Glottiphyllum, Hypertelis, Imitaria, Lampranthus, Lapidaria, Limeum, Lithops, Macarthuria, Mesembryanthemum, Mollugo, Nananthus, Odontophorus, Orygia, Pleisopilos, Plinthus, Polpoda, Psammotropa, Rhombophyllum, Rimaria, Ruschia, Semnanthe, Sesuvium, Tetragonia, Trianthema, Trichodiadema.

LITERATURE

On General Anatomy

Bolus 222, Brown, N. E. 291, Brown, Tischer, and Karsten 293, Huber 1104, Kean 1224, 1225, 1226, Kearney 1228, Kienholz 1236, Marloth 1444, Mullan 1571, Oberstein 1626, 1627, Oztig 1648, Pax and Hoffmann 1675, Pilger 1720, Reule 1925, Sabnis 1977, Schmid 2035, Schmucker 2042, Schwantes 2057, Summers 2221, Zemke 2505, Zwicky 2512.

156. UMBELLIFERAE

(FIG. 164 on p. 712; FIG. 165 on p. 714; FIG. 166 on p. 716; FIG. 167 on p. 718)

SUMMARY

(i) GENERAL

The family is mainly herbaceous, but includes a few species which tend to be woody. It occurs chiefly in temperate regions and on tropical mountains,

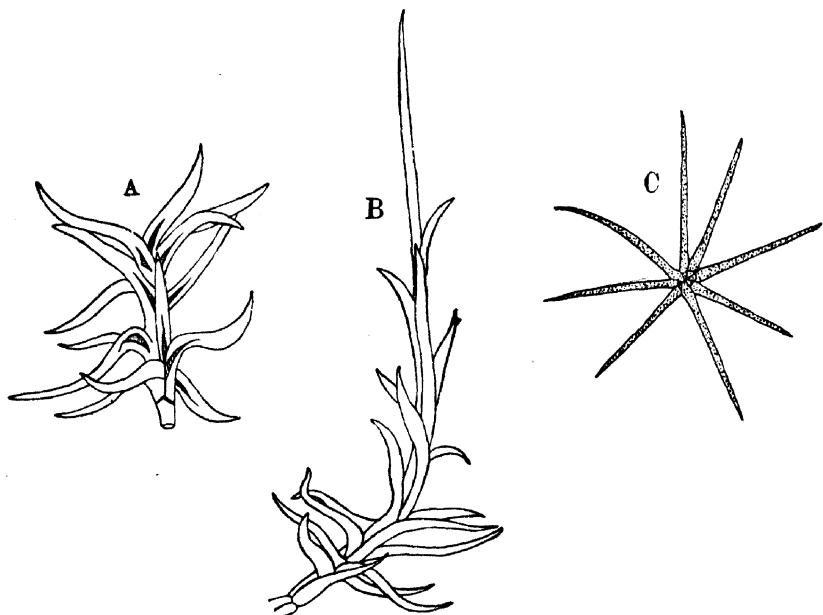


FIG. 164. UMBELLIFERAE

Trichomes of: A, B, *Xanthosia pilosa* Rudge; C, *Bowlesia tropaeolifolia* Gill. et Hook.—By Solereder.

but the various species grow in very different habitats. Some of the xerophytes show anatomical specializations ('Ecological Anatomy', p. 720). In spite of these ecological specializations, the basic structure is remarkably uniform throughout the family. The **stems** are often ribbed, whilst the centre is occupied by a pith which often becomes hollow apart from the septa at the nodes. The **ribs** on the stems usually consist of collenchyma, or, more rarely, of sclerenchyma. The **leaf** is usually dorsiventral, except in species which show ecological specializations. The **hairs**, which are nearly always non-glandular, include unicellular, dendroid, and stellate types. The **stomata** are sometimes accompanied by variously orientated subsidiary cells, but others are ranun-

culaceous. **Secretory canals**, which contain a mixture of oils, resin, and mucilage, are a particularly characteristic feature. They occur in the primary cortex, pericycle, pith, and sometimes the secondary phloem of the axis, but extend into the petiole and leaf lamina and also into the root. The **petiole** is usually provided with an arc or ring of vascular bundles, which sometimes surround medullary strands. In the stem there is always a ring of **vascular bundles**, which may be accompanied by medullary or, more rarely, cortical strands. The bundles of the main ring are sometimes embedded in sclerenchyma. **Anomalous secondary thickening** sometimes occurs in the stem and more frequently in the root. The anomalies include the development of numerous concentric bundles with central xylem; the formation of an extrafascicular cambial ring which produces xylem on the inside and phloem on the outside. A fissured xylem mass has been recorded in *Azorella*. **Crystals** are infrequent and often absent, but clusters and needles have been observed in a few species.

(ii) WOOD

Vessels very small to medium-sized, often in clusters and sometimes with a tangential pattern; perforations usually simple, but occasional scalariform plates sometimes present; intervacular pitting mostly alternate to opposite, sometimes almost scalariform, pits to parenchyma similar, sometimes simple; members of medium length to extremely short. **Parenchyma** paratracheal (scanty to vasicentric) and sometimes terminal. **Rays** usually up to 4-5 cells wide, sometimes more, heterogeneous to almost homogeneous. **Fibres** with simple pits, very to extremely short. **Intercellular canals** present in the rays of some genera.

LEAF

Usually dorsiventral, but centric in leaves having narrow or terete segments, e.g. in *Bupleurum* or *Foeniculum vulgare* Mill.; isobilateral in *Daucus carota* Linn. **Hairs** (Fig. 164) include the following types. (i) Simple, unicellular. (ii) Unicellular, bladder-like. (iii) Dendroid (Fig. 164 A-B), each having a few short basal cells and tiers of thick-walled ray cells with narrow lumina. (iv) Stellate (Fig. 164 c), with biseriate or multiseriate pedestals. (v) Small glandular hairs with 2- to 4-celled heads recorded on the lower side of the leaf of *Pimpinella saxifraga* Linn. Glandular hairs also reported from the peduncle of *Astrantia*, and on the umbels of *Heracleum*. Upper **epidermis** papillose in species of *Angelica*, *Anisotome*, *Bupleurum*, *Carum*, *Cicuta*, *Conium*, *Coriandrum*, &c.; consisting of specially large cells in *Hermas* sp. Epidermal cells surrounding the hair bases frequently forming cushions. **Stomata** occurring on both surfaces or confined to the lower side, differences in this respect being mainly of specific diagnostic value; arranged parallel to one another in species of *Eryngium* with a monocotyledonous habit. Rubiaceous stomata recorded in species of *Eryngium* and *Hydrocotyle*. Stomata ranunculaceous in species of *Ammi*, *Bowlesia*, *Caucalis*, *Conium*, *Coriandrum*, *Laserpitium*, *Mulinum*, *Peucedanum*, *Prangos*, *Sanicula*, *Seseli*, and other genera. **Hypoderm** recorded in species of *Aciphylla*, *Bupleurum*, *Eryngium*, &c. (see also 'Ecological Anatomy' on p. 720).

Vascular bundles of the **veins** nearly always accompanied above and

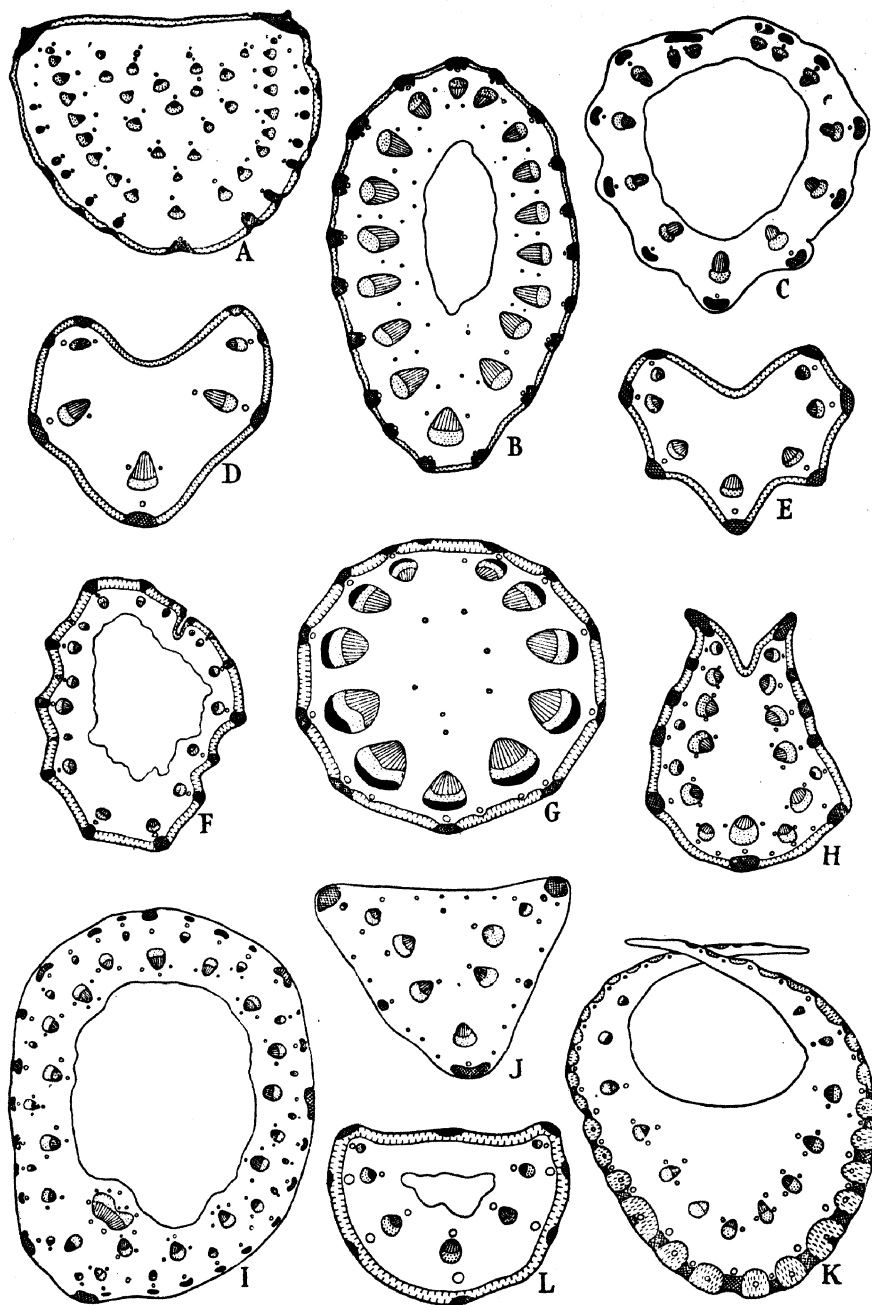


FIG. 165. *UMBELLIFERAE*

A, *Eryngium campestre* Linn. Petiole $\times 7$. B, *Foeniculum vulgare* Mil. Petiole $\times 8$. C, *Conium maculatum* Linn. Petiole $\times 7$. D, *Carum carvi* Linn. Petiole $\times 18$. E, *Apium graveolens* Linn. Petiole $\times 9$. F, *Oenanthe silaefolia* Bieb. Petiole $\times 13$. G, *Trinia glauca* (L.) Dum. Petiole $\times 18$. H, *Meum athamanticum* Jacq. Petiole $\times 15$. I, *Archangelica officinalis* Hoffm. Petiole $\times 7$. J, *Aegopodium podagraria* Linn. Petiole $\times 8$. K, *Crithmum maritimum* Linn. Petiole $\times 13$. L, *Seseli libanotis* (L.) Koch. Petiole $\times 33$.

The small unshaded circles represent secretory canals.

below or on one side only by collenchyma or parenchyma, the arrangement of which possesses diagnostic value. Sclerenchyma seldom present in the leaf, but recorded in association with the vascular bundles in *Eryngium campestre* Linn. and, according to Meyer (1509), between the marginal bundles and the actual margin in *Sanicula europaea* Linn.

Petiole, in transverse sections through the distal end of material examined at Kew, exhibiting a considerable range of structure (Fig. 165 A-L and 166 A, C, D, E, F, and H). Vascular bundles widely spaced and usually numerous, arranged in crescents, circles, or irregularly distributed in different genera and species. Various shaped crescents of bundles noted in species of *Aegopodium* (Fig. 165 J), *Apium* (Fig. 165 E), *Bupleurum* (Fig. 166 D), *Carum* (Fig. 165 D), *Chaerophyllum* (Fig. 166 H), *Coriandrum* (Fig. 166 F), *Crithmum* (Fig. 165 K), *Daucus*, *Echinophora* (Fig. 166 E), *Eryngium* (Fig. 165 A), *Falcaria*, *Meum* (Fig. 165 H), *Pimpinella*, *Sanicula* (Fig. 166 C), *Seseli* (Fig. 165 L), but additional medullary strands present within the crescent in *Chaerophyllum* (Fig. 166 H), *Daucus*, and *Eryngium*. Complete circles of separate bundles observed in species of *Archangelica* (double circle) (Fig. 165 I), *Conium* (Fig. 165 C), *Foeniculum* (Fig. 165 B), *Ligusticum* (Fig. 166 A), *Oenanthe* (Fig. 165 F), *Peucedanum* (double circle), and *Trinia* (Fig. 165 G). Numerous, scattered vascular strands present in *Ferula communis* Linn. and *Oenanthe crocata* Linn. Petiolar medullary bundles described by Solereder as initially collateral, or appearing to be bicollateral owing to the fusion of the xylem portions of 2 contiguous bundles. Centric medullary bundles sometimes formed from collateral strands by the development of xylem externally to the phloem. Sub-epidermal strands of collenchyma frequently occur opposite the peripheral vascular bundles of the petiole. **Secretory canals**, more fully described under 'Axis', present in the pith, pericycle, and cortex of the petiole, and in the phloem as well in certain species; in some species extending into the lamina beside the vascular bundles. These canals probably occur in all members of the family. Their arrangement in relation to the vascular bundles of the veins is said to be of specific diagnostic value. **Secretory cavities** also occur occasionally, e.g. in the mesophyll of *Aegopodium*. **Crystals** often absent, but, where present, generally clustered; recorded by Meyer (1509) in *Astrantia*, *Eryngium*, and *Sanicula*. Small, solitary or clustered crystals, of undetermined chemical nature, recorded, also by Meyer, in a few species of *Anethum*, *Angelica* (crystal-sand), *Apium*, *Foeniculum*, *Heracleum* (crystal-sand), *Levisticum*, *Petroselinum*, *Pimpinella*. Plumose masses of an unidentified material, probably hesperidin, also stated to occur in species of *Aethusa*, *Bupleurum*, *Chaerophyllum*, *Conium*, *Coriandrum*, *Cuminum*, *Oenanthe*, *Sium*, *Trinia*. Spherical aggregations of yellowish acicular crystals also noted at Kew in the epidermis and vessels of the petiole of *Crithmum maritimum* Linn. Tannin noted by Meyer (1509) in a few species of *Anthriscus*, *Chaerophyllum*, and *Siler*. For examples of special leaf structure see under 'Ecological Anatomy' on p. 720.

AXIS

STEM (Fig. 166 B, G, I, J, K)

Stems frequently with **ribs**, the latter consisting largely of collenchyma or, more rarely, of sclerenchyma; sometimes with palisade chlorenchyma between

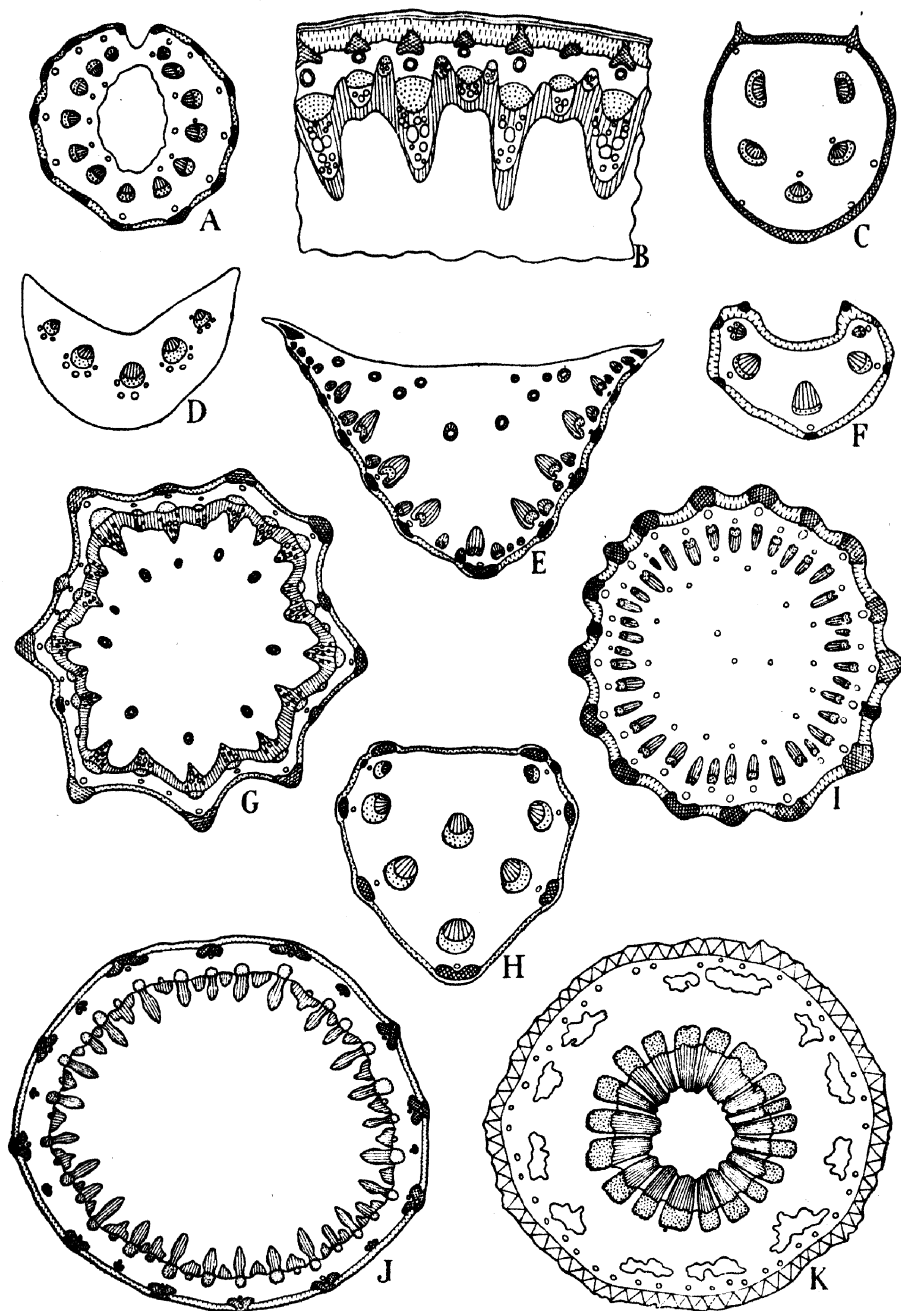


FIG. 166. UMBELLIFERAE

A, *Ligusticum scoticum* Linn. Petiole $\times 8$. B, *Foeniculum vulgare* Mill. Stem $\times 28$. C, *Sanicula gregaria* Bicknell. Petiole $\times 11$. D, *Bupleurum fruticosum* Linn. Leaf base $\times 11$. E, *Echinophora anatolica* Boiss. et Heldr. Petiole $\times 12$. F, *Coriandrum sativum* Linn. Petiole $\times 19$. G, *Apium graveolens* Linn. Stem $\times 8$. H, *Chaerophyllum nodosum* Crantz. Petiole $\times 12$. I, *Daucus hispidissimus* Sennen. Stem $\times 19$. J, *Smyrniolus olusatrum* Linn. Stem $\times 8$. K, *Crithmum maritimum* Linn. Stem $\times 15$, showing intercellular cavities in the cortex. The small unshaded circles represent secretory canals.

the ribs. A ring of collenchyma present beneath the epidermis in other species. Fine structure of the collenchyma of *Heracleum sphondylium* Linn. described in detail by Majumdar and Preston (1428). **Epidermis** sometimes sclerosed (see 'Ecological Anatomy' on p. 720). Apart from the chlorenchyma and collenchyma already mentioned in the primary **cortex**, the inner part of this region consists of thin-walled compact tissue with secretory canals embedded in it. **Cork** described by Solereder as originating in the sub-epidermis in *Bupleurum fruticosum* Linn., *Heteromorpha arborescens* Cham. et Schlechtd., and in species of *Hydrocotyle* and *Trachymene*; pericyclic in *Mulinum spinosum* Pers. Sub-epidermal cork recorded by Lemesle (1346) in *Hydrocotyle arbustula* Schlechtd., *Peucedanum capense* Sond., '*P. ferulaceum* Eckl. et Zeyh.', '*Trachymene ericoides* Sieber.', and '*T. linearis* Spreng.'. Cork described by the same author as arising in the inner part of the cortex in *Eryngium carlinoides* Boiss., *Hydrocotyle solandra* Linn., *Mulinum spinosum*, and *Pituranthos* spp. **Pericycle** sometimes including strands of fibres, but sclerenchyma in this region seldom well developed. **Vascular bundles** consisting mainly of primary tissue, and usually arranged in a ring, but accompanied by medullary or, less frequently, by cortical strands in some species. The bundles of the principal ring vary in size and distribution, and exhibit the following alternative arrangements. (i) Isolated bundles separated from one another by ground tissue. (ii) The xylem portions of the bundles united to one another by interfascicular, mechanical elements. (iii) Bundles wholly embedded in sclerenchyma. (ii) and (iii) occur particularly in xerophytic species. Vessels mostly with simple perforations; scalariform plates occasional (see 'Wood' on p. 719). **Medullary bundles** recorded in species of *Apium*, *Cachrys*, *Cenolophium*, *Crithmum*, *Eryngium*, *Ferula*, *Laserpitium*, *Magydaris*, *Oenanthe*, *Peucedanum*, *Pimpinella*, *Silau*, *Sium*, and *Thapsia*; their number varying considerably in different species; irregularly distributed or arranged in a ring; sometimes inversely orientated. **Cortical bundles** recorded in species of *Eryngium* with a monocotyledonous habit, as well as in *Siler trilobum* Crantz. and *Mulinum*. **Pith**. Central portion, in many species, becoming disorganized except for persistent septa at the nodes. Whole pith more durable and sometimes sclerified in species of *Coriandrum*, *Eryngium*, *Ferula*, *Sison*, *Sium*, &c.

Secretory canals, containing a clear, or turbid, milky-white or yellow mixture of oils, resin, and mucilage when fresh, present in the inner part of the primary cortex, as well as in the pericycle, and sometimes the secondary phloem of most if not of all members of the family. Secretory canals also occur at the periphery of or scattered in the pith of most members of the family, but none recorded in this tissue in a few species of *Bupleurum*, *Hydrocotyle*, *Xanthosia*; canals in the phloem occur particularly in woody species such as *Bupleurum fruticosum* and *Heteromorpha arborescens*. Canals in the aerial part of *Ferula communis* Linn. described by Perrot and Morel (1697) as consisting of those which are solitary except at the nodes and ramify in the parenchyma of the cortex and pith, and those accompanying and forking in the same way as the vascular bundles. Primary secretory canals in species of *Archangelica*, *Imperatoria* (*Peucedanum*), and *Levisticum* examined by Elias (625) said to arise in the pericycle, the later ones originating in tissue derived from the cambium. Layer of cells surrounding the cavity of the canals in the same genera described as producing mucilage, with fine cellulose threads

embedded in it. No resiniferous layer detected in these genera. Contents of the secretory canals of *Cicuta maculata* Linn. poisonous. According to Sifton (2097) the less poisonous nature of the aerial than of the underground parts of this plant is correlated with the smaller number of canals in the part of the plant above ground. Secretory canals in the cortex of *Smyrniun*

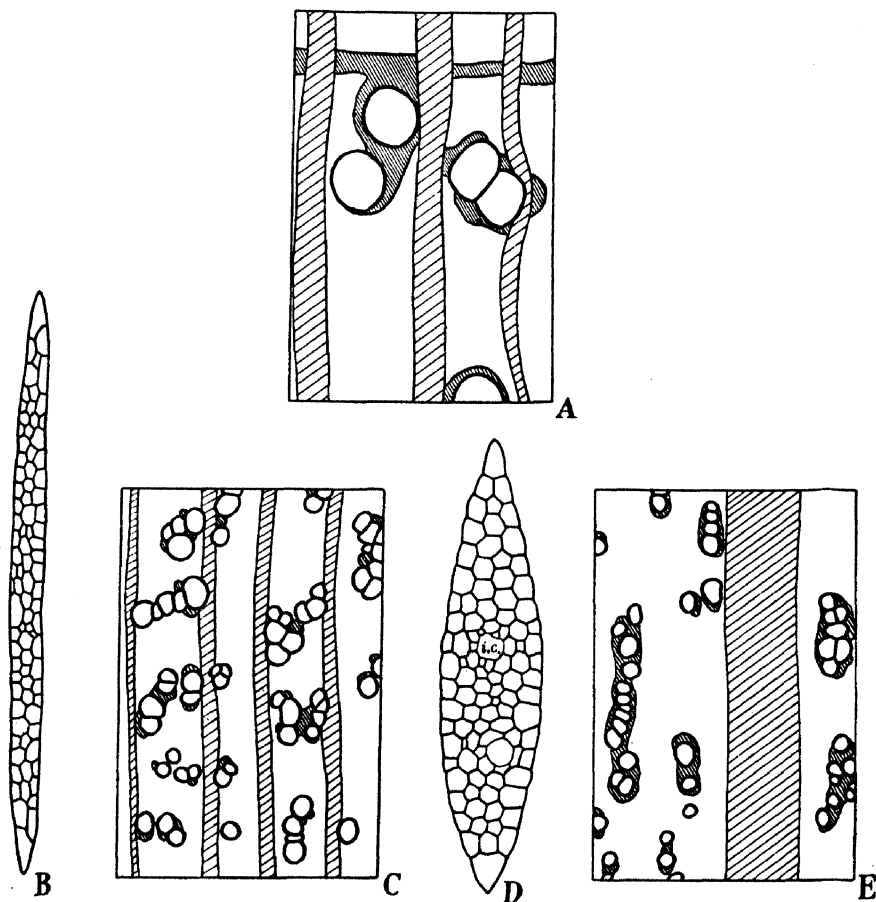


FIG. 167. UMBELLIFERAE

A, *Steganotaenia araliacea* Hochst. B, *Heteromorpha arborescens* Cham. et Schlecht. C, *H. arborescens* Cham. et Schlecht. D, *Steganotaenia araliacea* Hochst. E, *Eryngium inaccessum* Skottsberg.

i.c. Intercellular canal.

olusatrum Linn. seen at Kew to be in pairs, one being situated just outside and the other just inside each patch of collenchyma. For details concerning the development and mode of secretion of the canals in certain members of the family see Pirschle's (1726) paper. **Crystals** usually infrequent or lacking, mostly clustered when present. Clustered crystals noted at Kew in 2 species of *Eryngium* and acicular types in *Crithmum* and *Ferula*. **Developmental anatomy.** Details concerning the developmental anatomy of various mem-

bers of the family have been recorded by Brandscheit (256), *Chaerophyllum*; Majumdar (1424, 1425, 1427), *Heracleum*; Esau (651, 654), *Apium*.

WOOD (Fig. 167)

Vessels very small to medium-sized (mean tangential diameter ranging from 40 to 125 μ); often in clusters and with a tangential or oblique pattern (Fig. 167 c) in *Heteromorpha arborescens* (Thbg.) Cham. et Schlecht. and *Pituranthos* (1493); number per sq. mm. varying from about 5 in *Peucedanum* and *Steganotaenia* to 20–25 in *Eryngium* and *Heteromorpha*. Perforations typically simple, but occasional scalariform plates with few bars reported by Solereder to accompany the simple perforations in *Aethusa*, *Bupleurum*, *Carum*, *Hydrocotyle*, *Oenanthe*, *Peucedanum*, and *Xanthosia*.¹ Intervascular pitting usually alternate to opposite, the mouths of the pits horizontal and sometimes coalescing; often locally transitional between opposite and scalariform, particularly in *Heteromorpha*, in which the pitting is sometimes almost scalariform; pits to ray and wood parenchyma similar, sometimes simple. Mean length 0.25–0.45 mm. **Parenchyma** paratracheal, scanty to vasicentric, forming sheaths usually only 1 cell wide round the vessels; terminal bands observed in *Peucedanum* and *Steganotaenia*. Strands varying between 1–4 cells, e.g. in *Eryngium* and *Heteromorpha*, and 4–6, occasionally 8, cells, e.g. in *Peucedanum* and *Steganotaenia*. **Rays** usually up to 4 or 5 cells wide, up to 8 cells in some species of *Eryngium*; seldom more than 1 mm. high, except in some species of *Eryngium*; uniseriataes typically few and composed of both procumbent and square to upright cells, more numerous in *Eryngium bupleuroides* Hook. et Arn.; rays mostly between 2 and 8 per mm., more numerous where uniseriataes are common; usually slightly heterogeneous (Kribs's Type II B), with 1 or 2 marginal rows of square to upright cells; almost homogeneous in *Steganotaenia*, and composed almost entirely of square to upright cells in *Eryngium inaccessum* Skottsberg. **Fibres** with numerous, small, simple pits in the radial walls and few in the tangential walls; the pits larger and equally numerous on the tangential walls in *Eryngium inaccessum*; walls rather thin; mean length 0.3–0.75 mm. Majumdar (1422) has described the elongation of the fibres in *Heracleum* by 'intrusive' growth. **Intercellular canals** observed in the rays of *Eryngium*, *Peucedanum*, and *Steganotaenia*. Messeri (1493) refers to lysigenous secretory pockets ('tasche') in the rays of *Pituranthos*.

ANOMALOUS STRUCTURE

The development of an extrafascicular cambial ring, producing phloem on the outside and xylem on the inside, recorded in the stem of a few species of *Eryngium*. Transverse sections of the mature roots of certain species of *Angelica*, *Anthriscus*, *Apium*, *Carum*, *Chaerophyllum*, *Cicuta*, *Daucus*, *Magydaris*, *Oenanthe*, *Sium* exhibit numerous centric bundles, with central xylem, arranged in 2 or 3 concentric rings. The mode of development of this anomaly has been examined particularly in *Oenanthe crocata* Linn. In the young root of this species there are, around the pith, 5–14 groups of vessels, and between them a corresponding number of phloem strands. Each group

¹ Multiperforate plates have also been recorded by Majumdar (1421) in *Heracleum sphondylium* Linn., where they appear to be confined to the protoxylem of the leaves and the metaxylem in the nodal region of the stem.

of vessels becomes surrounded by cambial tissue, which forms a few new vessels and prosenchymatous elements on the inside; on the outside a considerable amount of parenchymatous tissue is produced. In this way the so-called centric bundles arise. A second ring of similar bundles then originates on the inside, and, by a repetition of this process, the structure of the mature root is attained. Secondary meristematic rings forming inversely orientated bundles recorded in *Myrrhis odorata* (Linn.) Scop. Xylem mass becoming fissured in *Azorella selago* Hook. f.

ROOT

Primary structure diarch in *Pimpinella* according to Michlin (1512). **Endodermis** with casparian thickenings recorded in the same genus. **Secretory canals**, similar to those of the stem and leaf, also occur in the root; those in the primary tissues said by Solereder to be situated immediately within the epidermis, opposite both the phloem and xylem groups of the vascular strand. Secretory canals in the primary tissues of *Pimpinella* described by Michlin (1512) as pericyclic. Canals also present in the secondary phloem of older roots of most members of the family; occurring in the xylem as well in species of *Myrrhis* and *Opopanax*. Perrot and Morel (1697) have recorded the following information concerning the root and rootstock of *Ferula communis* Linn. In the lower part of the root secretory canals are present in the pericycle immediately within the cork, and other canals in the secondary phloem. Transverse sections at higher levels in the root show more abundant secondary phloem and more numerous canals. Owing to pressure against the outer corky layer as growth in thickness proceeds, the primary and outer part of the secondary phloem is crushed and the medullary rays become sinuous. The canals in the crushed tissue likewise become compressed, but the pericyclic canals, protected by the cork, persist. In the upper part of the rootstock, where a pith is differentiated, the xylem parenchyma and rays become mucilaginous, and the groups of vessels can be seen in the partly disorganized tissue. At a still higher level, transverse sections show the xylem as part of a ring of vascular bundles separated by wide medullary rays. The centre of the rootstock in this region is occupied by a cavity, surrounded by an internal layer of cork. The secretory canals are solitary in the lower but anastomose in the upper part of the root. Lunan (1401) refers to convoluted, radiating strands of amyloiferous tissue in the adult root of *Ligusticum scoticum* Linn. due to unequal strains set up between the rigid xylem and the confining cork tissue. The structure of the **contractile roots** of various members of the Umbelliferae in relation to their physiological function has been described by Berckemeyer (175). The root structure of carrot seedlings has been described by Havis (922), and the **developmental anatomy** of the carrot by Esau (654).

ECOLOGICAL ANATOMY

Several authors have drawn attention to the structural plasticity of certain members of the Umbelliferae. Funk (733), for example, has pointed out that the distribution of collenchyma and other mechanical elements in umbelliferous stems is liable to vary in response to environmental factors, to undetermined causes, or at different stages in the development of the plant.

The arrangement of the mechanical tissue is, therefore, of restricted diagnostic value. Mokeeva (1546) found that the stem structure of certain species of *Muretia* and *Scaligeria* varies so much in plants growing under different ecological conditions that the genera cannot be distinguished by the microscopical features of the stem. All of the stem tissues in each individual species are also very plastic. Lunan (1401) has demonstrated that the uppermost leaf of *Ligusticum scoticum* Linn. is more xerophytic than the remainder.

Friedel and Yen (719) made an anatomical comparison between *Eryngium campestre* Linn. and *Drypis spinosa* Linn. (family Caryophyllaceae). These 2 xerophytes, although wholly unrelated in the taxonomic sense, show a superficial resemblance to one another. Friedel and Yen showed, however, that both species are anatomically similar to the family to which each belongs, thus demonstrating that the hereditary anatomical characters are not profoundly modified by environment.

Lemesle (1346) made a comprehensive study of the stem structure of xerophytic members of the family from different parts of the world. The following information is taken from the summary of his long, detailed article. The epidermis is provided with a thick cuticle, or, in certain species from the Mediterranean region, steppe regions, Chile, and Australia, the whole epidermal layer becomes completely sclerosed. The collenchyma of the primary cortex is sometimes strengthened or wholly replaced by fibres, whilst, in certain species of *Eryngium* from the Mediterranean region, the fibres form a continuous cylinder. In other species, e.g. *Chamaerea capensis* (Thunb.) Eckl. et Zeyh. (syn. *Carum capense* Sond.) and some Australian members of the family, although the cortical collenchyma is reduced or absent, there are sub-epidermal fibres which are either widely spaced or form an almost continuous ring. In other species the ground tissue of the cortex tends to become sclerified, this feature being particularly well developed in *Apium panul* (Gay) Reiche var. *araucarum* (Phil.) Reiche (syn. *Ligusticum pansil* Bert.) from Chile. A sclerified cortex was not found in species from Australia, but is common in those from steppe regions. The cork is sometimes especially well developed, and constitutes a cylinder of mechanical tissue. This occurs in species of *Eryngium*, *Hydrocotyle*, *Mulinum*, *Peucedanum*, *Pituranthos*, and '*Trachymene*' from the southern hemisphere, particularly South Africa and Australia, in some of which the cork arises in the sub-epidermis, but in others from the inner part of the cortex (see 'Stem' on p. 717). Certain members of the family from steppe regions have the cortex reduced to 2 or 3 layers of small cells. Lemesle, after pointing out that the pericycle nearly always includes arcs of fibres, that the xylem and phloem, particularly in species from South Africa and Australia, are in the form of continuous cylinders or have fibrous interfascicular tissue, that the pith is often persistent, reduced in size, and sclerified, ends by pointing out that the secretory canals, especially those in the pericycle, are often more numerous and of larger diameter in xerophytes than in species growing where the climate is less severe.

Chodat and Vischer (402), who examined the anatomy of various Umbelliferae from Paraguay from the ecological standpoint, found an interesting range of structure in different species of *Eryngium*, especially in those with a habit recalling that of the monocotyledons. In this genus there are species with xerophytic and others with hygrophytic features, whilst in a third category

there is a mixture of characters of both kinds. Thus in *E. paniculatum* Cav. there is an almost continuous zone of hypodermal sclerenchyma—a xerophytic feature—combined with large intercellular spaces in the mesophyll as is characteristic of hygrophytes. Xerophytic features are especially well developed in *E. hassleri* Wolff. and related species with grass-like leaves. Here the leaf area is reduced, palisade tissues are developed below all parts of the surface, and hypodermal fibres are numerous. *E. sanguisorba* Cham. et Schlecht., with leaves like those of *Luzula* or *Plantago*, also exhibits xerophytic characters, but of a rather different kind. Here there is no hypoderm, but the cuticle is very thick; there are no lacunae in the mesophyll, which is supported by strands of fibres radiating outwards from the aqueous tissue around the vascular bundles. Hygrophilous forms include *E. floribundum* Cham. et Schlecht. var. *serrioides* Urb., belonging to the taxonomic group *areata*. Here the cuticle is thin, the hypoderm is not sclerified, and the palisade tissue is in direct contact with the upper epidermis. In *E. pandanifolium* Cham. et Schlecht., another hygrophyte, sclerosed hypoderm occurs beneath each epidermis, there is assimilating tissue towards each surface, whilst the mesophyll includes large intercellular spaces.

Chodat and Vischer's work provides an interesting addition to Solereder's earlier statement that species of *Eryngium* with a monocotyledonous habit are provided with longitudinal air canals, interrupted at intervals by transverse diaphragms, whilst the vascular bundles, mostly in pairs of which the upper member is inversely orientated, lie longitudinally in the tissue between the air canals. Solereder also records that in some species of *Eryngium*, broad strips of palisade tissue, alternating with narrower strips of sclerenchyma, occur below the epidermis or hypoderm towards both surfaces of the leaf. Solereder also notes that *Foeniculum vulgare* Linn. has a leaf which, in transverse sections, is circular in outline, with an envelope of palisade tissue beneath the epidermis, locally interrupted by bundles of collenchyma. The centre of the leaf in this species is occupied by a ring of vascular bundles on the same radii as the collenchyma.

For further details concerning the species of *Eryngium* with a monocotyledonous habit see Wolff's (2453) summary of Moebius's earlier work.

The ecological anatomy of '*Anisotome aromaticum* Hook. f.' has been described by Betts (188).

TAXONOMIC NOTES

Hoar (980) found the anatomical resemblances between the Araliaceae and Umbelliferae to be closer than those between either of these families and the Cornaceae. He therefore proposed that the Cornaceae should not be included in the same cohort as the other 2 families. The fundamental similarity between the Araliaceae and Umbelliferae has also been confirmed at Kew by Dr. C. L. Hare. Amongst the more important resemblances he noted are the following. The principal mechanical tissue in young stems of both families is in the form of peripheral collenchyma, pericyclic sclerenchyma being scanty or absent. Thin-walled, aqueous tissue is abundant in the stems of both families. Although secretory cells were not observed in either family, similarly distributed secretory canals occur in both. Except in *Dizygotheca* no solitary crystals were observed in either family. Medullary vascular bundles occur in

several genera of both families. Wherever these occur they are often collateral and inversely orientated, or more or less centric with central xylem. The range of vascular structure in the petioles of the 2 families is also very much alike, types with numerous scattered bundles or with the vascular strands arranged in 1 to several rings being the most frequent. Differences noted between the 2 families are mainly those correlated with the more woody character of the Araliaceae as compared with the dominant herbaceous habit in the Umbelliferae.

Majumdar (1421) attaches no phylogenetic significance to the multiperforate perforation plates which he observed in the primitive, spirally thickened vessel members in the protoxylem of leaves and in the more specialized, pitted vessel members which occur in the metaxylem of the nodal regions of stem of *Heracleum sphondylium* Linn.

ECONOMIC USES

Certain members of the Umbelliferae are eaten as vegetables, others are the source of gum-resins used in perfumery and medicine, and a third group yield other products of medicinal value. Serious cases of poisoning have been caused by a few species.

Familiar vegetables, derived from cultivated varieties of species belonging to this family, include the carrot (*Daucus carota* Linn.), the parsnip (*Pastinaca sativa* Linn.), celery (*Apium graveolens* Linn.), and parsley (*Petroselinum crispum* (Mill.) Nym.). Angelica, prepared from the stems of *Archangelica officinalis* Hoffm., is used in confectionery. The anatomy of the vegetative organs of the parsnip has been described in some detail by Warning (2363), who showed that the mature 'root' consists of the true primary root and the hypocotyl. Most of it is built up of amyliiferous phloem parenchyma, the central part being occupied by xylem, and, in the region of the hypocotyl, a pith. The primary structure is diarch, although apparently triarch roots are known. The oil ducts in the pericycle and primary phloem are relatively ephemeral. The floral axis, initiated during the first year, develops rapidly during the second. Hayward (927) has also described the anatomy of *Apium graveolens*. According to Lambeth (1315) the medullary bundles of *Apium graveolens* are cauline in nature, they may arise and terminate at any level in the stem, and have no connexion with the leaf traces. The occurrence of roots in the internal cavities in a celery 'tuber' has been described by Fourcroy (699). A seedling carrot with an abnormal cotyledon was investigated by Parrot (1656), and the results of other work on the seedling anatomy of the carrot published by Fourcroy (698) and Havis (922). For developmental anatomy of the carrot see Esau's (654) article.

Gum-resins derived from this family include galbanum (*Ferula galbaniflua* Boiss. et Buhse and other species of *Ferula*); asafoetida (*Ferula foetida* Regel and other species of *Ferula*); ammoniacum (*Dorema ammoniacum* D. Don). All of these are obtained from Iran and adjacent regions. Moroccan ammoniacum is said to be derived from *Ferula communis* Linn. var. *nodiflora* Linn., and Cyrenian ammoniacum from *F. marmarica* Aschers et Taub.

Caraway seeds and oil are obtained from *Carum carvi* Linn., which is cultivated in many parts of Europe; the fruits of *Peucedanum graveolens* Benth. yield an oil used in the preparation of dill-water; oil from the fruits

and leaves of fennel (*Foeniculum vulgare* Mill.) is employed for flavouring and in medicine, whilst aniseed (the seeds of *Pimpinella anisum* Linn.) is also valued in medicine. The oil from *Coriandrum sativum* Linn. is used for flavouring and in veterinary medicine.

Sumbul, which consists of pieces of the dried rhizome and rootstock of *Ferula sumbul* Hook. f. and probably of *F. suaveolens* Aitch. et Hemsl., obtained from Turkestan, was at one time valued in medicine, but is not now much employed. The commercial article consists of pieces about 3–6 cm. long and wide. The brown to black outer surface is transversely wrinkled, whilst fibrous leaf-trace bundles project from the scars of fallen leaves. Transverse surfaces exhibit, internally to the thin layers of cork and bark, a ring of yellowish vascular bundles, and additional medullary strands scattered irregularly in the parenchymatous ground tissues in which resinous material is also deposited.

Numerous other Umbelliferous plants have been used in folk medicine, but are now unimportant. The root anatomy of 28 such species has been described by Liermann (1370). According to Michlin (1512) the roots of *Pimpinella saxifraga* Linn. can be distinguished from those of other members of the Umbelliferae with which they might be confused by the fact that the cells of the medullary rays are not radially elongated.

Members of the family with poisonous properties include *Conium maculatum* Linn., *Oenanthe crocata* Linn., &c.

GENERA DESCRIBED

(i) FOR GENERAL ANATOMY

Aciphylla, Aegopodium,* Aethusa, Ammi, Anethum, Angelica,* Anisotome, Anthriscus, Apium,* Archangelica,* Astrantia, Azorella, Bowlesia, Bupleurum,* Cachrys, Carum,* Caulis, Cenolophium, Chaerophyllum,* Cicuta, Conium,* Coriandrum,* Crithmum,* Cuminum, Daucus,* Echinophora,* Eryngium,* Falcaria,* Ferula,* Foeniculum,* Heracleum, Hermas, Heteromorpha, Hydrocotyle, Laserpitium, Levisticum,* Ligusticum,* Magydaris, Meum,* Mulinum, Muretia, Myrrhis,* Oenanthe,* Opopanax, Petroselinum, Peucedanum,* Pimpinella,* Pituranthos, Prangos, Sanicula,* Scaligeria, Seseli,* Silaus, Siler, Sison, Sium, Smyrnum,* Thapsia, 'Trachymene', Trinia,* Xanthosia.

* Represented in the Kew slide collection.

(ii) FOR WOOD STRUCTURE

(Aethusa), (Bupleurum), (Carum), Eryngium, Heteromorpha, (Hydrocotyle), (Oenanthe), Peucedanum, (Pituranthos), Steganotaenia, (Xanthosia).

LITERATURE

(i) On General Anatomy

Berckmeyer 175, Betts 188, Brandscheit 256, Buchet 304, Chodat and Vischer 402, Elias 625, Esau 651, 654, Fourcroy 698, 699, Friedel and Yen 719, Funk 733, Guérin 837, Havis 922, Hayward 927, Hector 929, Hoar 980, Lambeth 1315, Lemesle 1346, Liermann 1370, Lunan 1401, Majumdar 1421, 1424, 1425, 1427, Majumdar and Preston 1428, Meyer 1509, Michlin 1512, Mokeeva 1546, Parrot 1656, Perrot and Morel 1697, Pirschle 1726, Schwarz 2058, Sifton 2097, Tunman 2292, Turmel 2299, Warning 2363, Wolff 2452, 2453, 2454.

(ii) On Wood Structure

Hoar 980, Majumdar 1422, Messeri 1493, Record 1843, 1851.

